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MORPHOLOGY AND TAXONOMY OF THE NEW WORLD SPECIES OF *MAIANthemum* (LILIACEAE)

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This paper presents a morphological study, including a revised taxonomy, of the fifteen New World species of *Maianthemum* Wigg. and is preliminary to a world-wide taxonomic revision and phylogenetic analysis of the genus.

The species of *Maianthemum* can be divided into three geographically defined groups: North American, distributed from the arctic to just beyond the Rio Grande; Central American, growing from the state of Mexico to western Panama; and Eurasian, most of which are found in eastern Asia. Most species of *Maianthemum* are restricted to one of the three regions, and the centers of taxonomic diversity for the genus are in eastern and western Canada, Guatemala, and southern China. However, the present study is focused not so much on geography as it is on vegetative morphology, which is very diverse among the many species. A novel aspect is the emphasis placed on the individual shoot as the basic unit of form and growth. The first portion of the shoot, the rhizome, is given special attention, which is significant in two respects. Taxonomically, the rhizome exhibits numerous features that distinguish species decisively, often even when features of the leaves and flowers are ambiguous. Also, the rhizome is ecologically important because it is the perennial portion of the plant, an organ of nutrient and water storage, and the source of renewal buds that extend the life of the individual.

Maianthemum is clearly separated from allied genera in the tribe Polygonatae in having the combination of a simple aerial stem, a morphologically distinctive terminal inflorescence, spotting on immature berries, and a haploid chromosome number of 18. The clarity of the generic limits has been appreciated by only a few previous authors, and most modern floras divide *Maianthemum* into a pair of closely allied genera, *Maianthemum* and *Smilacina* Desf. The division is based on the number of floral parts: the 25 species with trimerous

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flowers (six tepals, six stamens, three carpels) typical of the Liliaceae are placed in *Smilacina*, whereas the three species with dimerous flowers (four tepals, four stamens, two carpels) are placed in *Maianthemum* sensu stricto. Earlier (LaFrankie, 1986), I assembled comparative data for the genera in the Polygonatae and demonstrated that *Maianthemum* sensu lato is distinguished from all allied genera by a singular combination of morphological traits, including a unique karyotype, whereas the dimerous and trimerous species are separated from one another by only a single derived feature. I then recommended that *Maianthemum* and *Smilacina* be combined under *Maianthemum*, which is the older name. Despite the number of species involved and their familiarity to botanists of the Temperate Zone, the possibility of conserving the name *Smilacina* was rejected. The transfers did not obscure the older literature, nor did they complicate current taxonomic research, which is chiefly Neotropical and Asian. Therefore, in consequence of this broader—although still traditional—view, the present study is the first modern taxonomic work to treat both the dimerous and trimerous species under the same generic name.

Because some of the species in this genus are well known under the name *Smilacina*, a further note on the new combinations is appropriate. While it is possible that the dimerous species originated prior to the 25 trimerous species and thereby merit consideration as a distinct genus, there is no evidence to support such a scenario. Much to the contrary, it appears on morphological grounds that the dimerous species are most closely related to sympatric trimerous species of the North Temperate Zone. In vegetative form, growth habit, distribution, and inflorescence architecture, at least one trimerous species, *Maianthemum trifolium*, bears a greater resemblance to the dimerous species than it does to the large paniculate species of the Tropics. In summary, the evidence presented within this work and in the earlier note (LaFrankie, 1986) indicates that under no circumstances would the combination of the dimerous and trimerous species be discordant with phylogeny, but separation of the groups most likely would be. Other details of generic nomenclature are published in the earlier note (LaFrankie, 1986).

The nomenclatural history of the individual North American species is somewhat complicated because many generic synonyms have been published. By contrast, the taxonomic history of these species is relatively clear. In *Species Plantarum* Linnaeus (1753) recorded three of the five species now known from North America. He was probably unfamiliar with the dimerous species from the northwestern part of the continent, *Maianthemum dilatatum*, and he considered the dimerous plant of the northeastern section, *M. canadense*, to be conspecific with the Eurasian *M. bifolium* (L.) F. W. Schmidt. After the two dimerous species of North America were recognized during the early 1800's, the taxonomy of the species indigenous to temperate North America remained rather uncontroversial, except perhaps the work of Greene (1889), which contained several new species and dozens of manuscript epithets for *M. stellatum* and *M. racemosum* (discussed under the individual species). My treatment does not differ in any major point from the most recent studies (Galway, 1945; Ingram, 1966), other than in using new combinations based on *Maianthemum* for the trimerous species.

However, this paper does address several taxonomic issues concerning the species of *Maianthemum* in Central America. The monographic treatment of the genus by Baker (1875), under the name *Tovaria* Baker, is now much outdated, as is the revision of that work by Hemsley (1879–1888). The most recent taxonomic revision was by Emons (1945). Although his study was limited to herbarium material, he made good use of the collections of Standley and Steyermark from Guatemala, and his species descriptions—with the exception of the overly inclusive *Smilacina paniculata*—are generally sound. However, recent and extensive collections from Veracruz, Chiapas, Costa Rica, and Panama have provided numerous specimens that illustrate the difficulty of distinguishing among *Maianthemum scilloideum*, *M. flexuosum*, and *M. amoenum*. This paper clarifies the distinctions and also presents an analysis of the diverse plants with paniculate inflorescences.

MORPHOLOGY

GROWTH HABIT

The identification of species in *Maianthemum* is based largely on the morphology of the floral shoot, knowledge of which requires an understanding of shoot development. The study of growth habit therefore plays an important role in the taxonomy of this genus. In *Maianthemum*, as in many monocotyledons, the fundamental unit of organization is the individual shoot axis. Each shoot is relatively short lived by virtue of its terminal inflorescence, but the life of the plant is extended indefinitely through the early development of renewal shoots from lateral buds located at the base of older shoot axes (see FIGURE 1). This serial replacement of short-lived determinate shoots is termed “sympodial growth” and is characteristic of all species of *Maianthemum*, as well as all other genera in the tribe Polygonatae. Despite the similarity of growth habit, the individual species differ markedly in morphological details.

Each shoot consists of three discrete portions: a rhizome, a leafy stem, and a terminal inflorescence. Although these sections are entirely distinct, they are not separate organs but represent different developmental stages of a single shoot. Each shoot commences with a rhizome that grows horizontally, carrying the apex clear of the parent shoot and then turning upward to produce the leafy portion. A terminal inflorescence completes the development; thereafter, the aerial portion usually abscises from the persistent rhizome portion. (A more detailed analysis of shoot morphology and development is presented in LaFrankie, 1984, 1985b.)

Maianthemum goes through a stage of establishment growth similar to that seen in other Liliaceae (Barton & Schroeder, 1942; Barton, 1944; LaFrankie, 1985a). Germination is hypogeal, the cotyledon remaining within the seed as the primary shoot axis develops at the cotyledonary node. The first foliar elements are scale leaves, followed by a single foliage leaf supported by an elongate petiole. Petiolate foliage leaves replace one another in succession as the primary seedling axis grows in diameter; ultimately, the primary axis produces a pair of sessile foliage leaves supported by an extended aerial stem, and

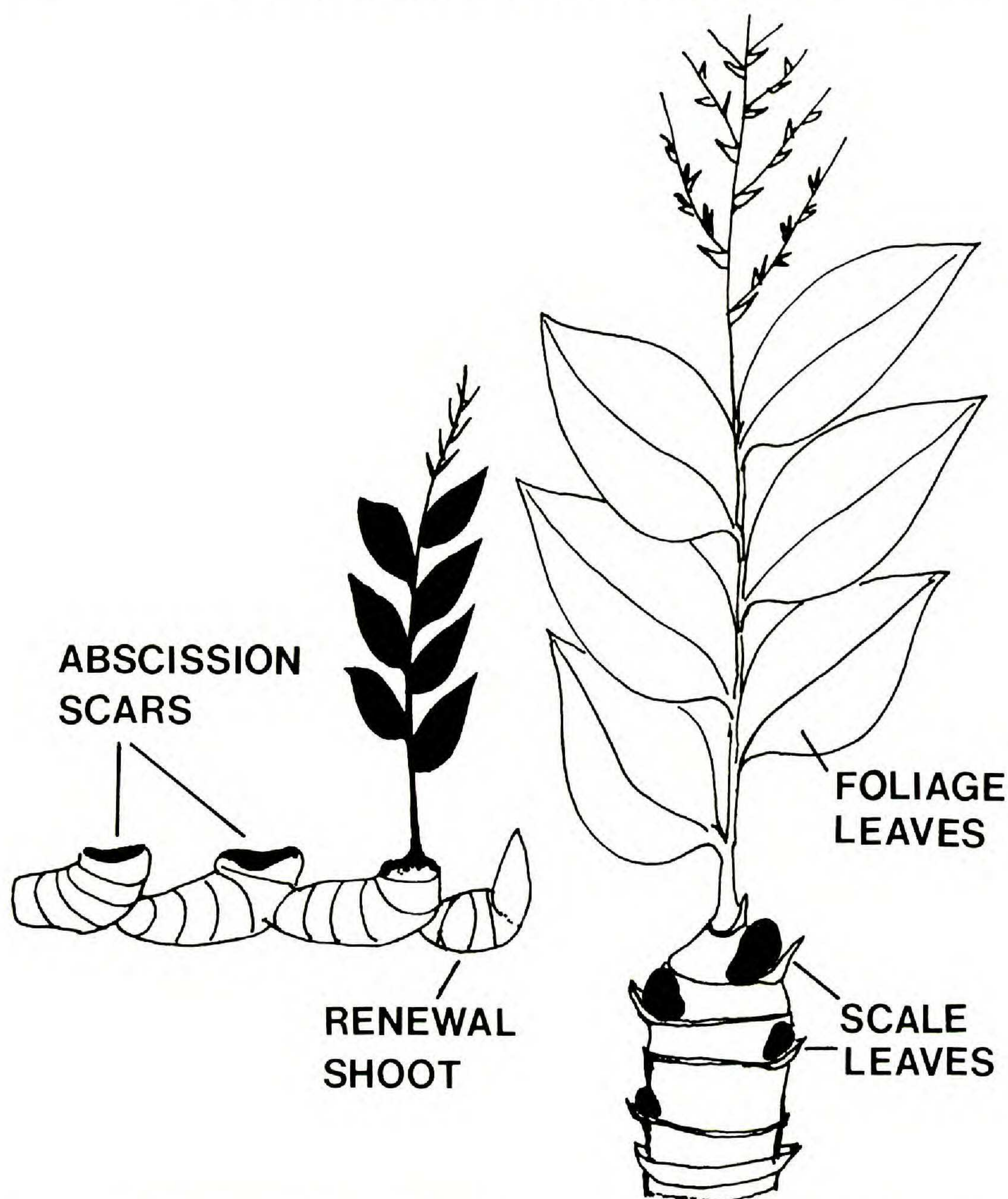


FIGURE 1. Shoot morphology in *Maianthemum*. Individual shoots determinate, growth through sympodial renewal; each shoot comprising persistent rhizome portion and short-lived aerial shoot (lost through abscission). Rhizome portion bears scale leaves, lateral buds ranked acropetally in size, and roots (not shown); aerial portion bears foliage leaves without axillary buds; inflorescence bears bracts subtending single flowers or extended racemes.

thereafter adult or renewal growth commences as renewal shoots are produced from axillary buds on the lower portion of the parent stem.

There are four different patterns of shoot development in *Maianthemum*, but they share several features. In all species of *Maianthemum*, the two growth processes of initiation and extension are separated temporally. All appendicular parts are initiated in miniature within a swollen renewal bud and then reach full size through uninterrupted meristematic growth and cell enlargement. In

the first type of growth, shoot development is both complete (meaning that all leaves and flowers are produced at once) and seasonal. This type of growth is typical of spring emergents of the Temperate Zone, such as *M. racemosum*, but it is also found in the seasonal environments of the tropical mountains, in which case the renewal shoot usually extends during the dry season (January–March). In the second type of growth, shoot development is also complete, but shoots are initiated more or less continuously and without strict regard to the season. This type is found in tropical plants of some lower montane areas in which seasonality is less pronounced. The third and fourth types of shoot growth involve intermittent rather than complete development. Among the New World species, only *M. trifolium* exhibits the third type of growth: a pair of petiolate foliage leaves is produced in the first growing season, and an extended floral stem bearing two to four sessile foliage leaves during the second. The fourth growth type is shown by *M. dilatatum* and *M. canadense*; it is quite similar to the third, differing in that only a single petiolate leaf appears during the first growing season. This vegetative phase may continue for as many as six subsequent growing seasons before a floral shoot is produced (Kana, 1983). That the third and fourth types of growth correspond in many details to the process of establishment growth (LaFrankie, 1985a) is perhaps indicative of their neotenic origin.

ROOTS

In *Maianthemum*, root meristems are initiated near the rhizome apex as part of primary growth, so the number of roots on a stem is fixed early in development—new roots cannot grow from old stems. This constraint is important since lost roots can be replaced only through the development of new rhizomes, which is a seasonal phenomenon for many species.

Roots in *Maianthemum* are of limited taxonomic significance. Their anatomy is quite uniform: each has a broad cortex lacking storage products, a sclerized pith lending mechanical support, and vessels in the xylem. Some species can be recognized by the dimensions of the roots and by their distribution along the rhizome. Normally, roots occur all over the rhizome at nodes and internodes and are especially numerous at the base of the leafy stem, but *M. stellatum* has dimorphic roots with many small roots scattered along the stem and a few larger ones aggregated near the shoot base, and *M. trifolium*, *M. canadense*, and *M. dilatatum* have roots restricted to the nodes.

RHIZOME

In the past the term rhizome has been applied to various plant parts (see Holm, 1929; Bell & Tomlinson, 1980), often with little thought or regard for precise terminology. In the shoot system of *Maianthemum*, the rhizome is the perennial branching portion that bears roots, scale leaves, and lateral buds. The transition from rhizome to leafy stem is discrete and, in most species, clearly demarcated by a long internode commencing the aerial portion. The leafy stem is further distinguished in having an epidermis instead of a periderm, in having collateral instead of amphivasal vascular bundles, and in lacking

axillary buds and roots. In most species of *Maianthemum*, the rhizome portion of the shoot persists for several shoot generations, accumulating to form an often-extensive branching aggregate. In this paper I use "rhizome" to describe this sympodial aggregation, and "individual rhizome unit" to describe the rhizomatous portion of a single shoot.

In form and habit rhizomes in *Maianthemum* are diverse: in some species they are extended and stoloniferous, while in others they are swollen and tuberous; they may be subterranean, aquatic, or fully exposed; they may even be orthotropic as in *M. paludicolum*. Most species are easily distinguished by their rhizomes alone, using features such as number of scale leaves, distance between internodes, number of lateral buds and their plane of insertion, and type and distribution of storage products.

In general, scale leaves of the rhizome are distichous and are inserted in a plane parallel to the ground, although in fact the planes of insertion of right and left scale leaves form a slight dihedral angle toward the stem's lower side. Most often, lateral buds are axillary, but in some species they may be initiated in eccentric positions, toward either the midpoint of the internode or the lower side of the rhizome. This has the effect of creating a linear rather than a forking sympodium, a situation that also occurs in *Croomia* Torrey & A. Gray (Tomlinson & Ayensu, 1968) and *Podophyllum* L. (Holm, 1899). In all species of *Maianthemum*, the lateral buds are acropetally ranked in size, and usually the one or two buds nearest the foliar stem portion form the subsequent renewal shoots, while those more distal remain dormant.

The carbohydrate reserves of *Maianthemum* and their patterns of deposition are evidently quite diverse and merit a thorough investigation. With regard to the storage of starch (as identified microscopically and with IKI), I have made observations on fresh rhizomes in most species and have extended these observations using rhizomes preserved in FAA. In some cases material from only one collection site was available for study, but in all instances several plants could be compared. In all, I discovered four patterns of starch deposition within the genus. 1) Starch may be absent entirely from all portions of the rhizome, as in *M. gigas*. 2) If starch is abundant in the developing rhizome, it may be depleted slowly over the course of three or four years, after which the rhizome decays, as in *M. stellatum*. 3) Alternatively, starch in a developing rhizome may be depleted very quickly, even before the renewal bud fully forms, and then remain absent, replaced in part by a thick mucilage, as in *M. racemosum*. 4) Having been initially depleted, starch may again accumulate in the distal portions of the rhizome, first in the fully developed cortex and then across the entire central cylinder, as in *M. flexuosum*.

LEAFY STEM

The leaf-bearing portion of the stem is roughly similar—at least in general aspect—in all species of *Maianthemum*, and this can make identification of vegetative material difficult. Differences among species often include stem and leaf dimensions, but these vegetative differences can be obscured by the developmental stages through which growing individuals pass. As a plant grows,

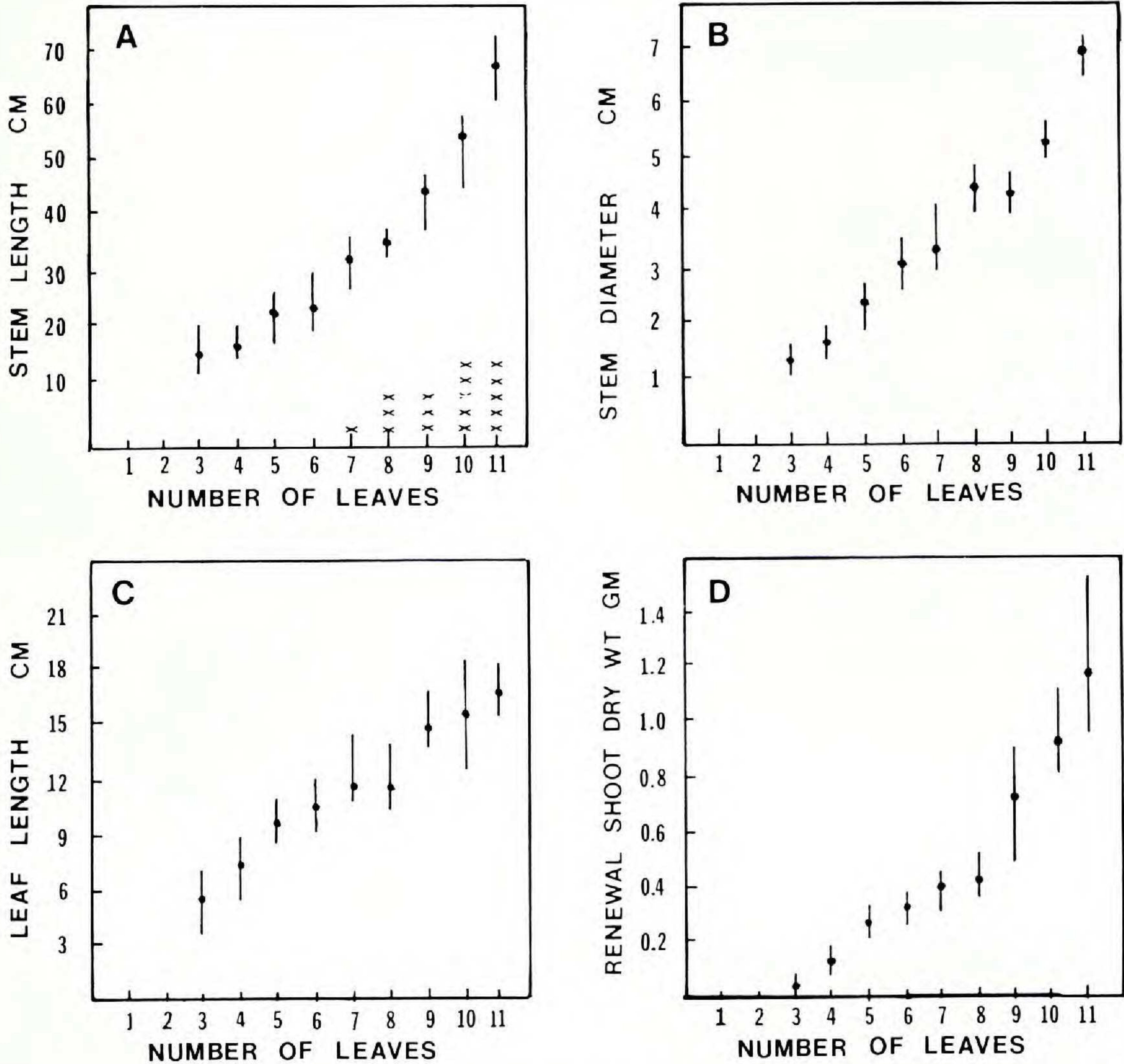


FIGURE 2. Relationship between morphometric features and number of foliage leaves on shoot (showing coordinated increase in size accompanying sympodial growth): A, length of aerial stem (reproductive individuals indicated by x's); B, aerial-stem diameter at base; C, length of the penultimate foliage leaf; D, dry weight of primary renewal shoot separated from base of aerial stem bearing indicated number of leaves. Data are mean and range of sample, indicating great constancy within each leaf-number class. Based on 5 randomly chosen individuals per leaf-number class, from natural population of *Maianthemum racemosum* subsp. *racemosum*, in Medford, Massachusetts.

larger shoots replace smaller ones, and the dimensions of the leaves and stem increase with each new shoot in a way that is consistent within a species. That is, for plants growing under more or less uniform conditions, there is a close correlation among morphometric features, including the number and dimensions of foliage leaves, the length and diameter of the stem, the dry weight of the renewal shoot, and the initiation of an inflorescence. In *M. racemosum*, for example, various morphometric features are closely correlated with the number of foliage leaves borne on a stem (see FIGURE 2). Due to the architectural similarity of the different species and the role that reduction has played in their evolution, small shoots of characteristically large species can sometimes be

confused with full-sized shoots of smaller species. A general rule of thumb is that a plant has not reached its full size until the inflorescence is longer than the penultimate foliage leaf.

In each species of *Maianthemum*, the leafy shoot has a characteristic habit or posture. The stem may be stiff and straight or slightly flexuous; it may be upright, pendent, or arching so as to display the foliage leaves in a plane. The habit can sometimes be useful in distinguishing between taxa, such as the upright and arching subspecies of *M. racemosum*.

The surface of the lower portion of the foliar stem is usually smooth and sometimes is even polished, whereas that of the upper portion may be sculptured with small ridges or distinct ribs sometimes bearing denticles or fine hairs. While the indument is rather variable within and among species of *Maianthemum* (as discussed under the section on leaves), the ribbing is a relatively consistent feature.

LEAVES

Foliage leaves in *Maianthemum* are simple and most often ovate, although they range from obovate or elliptic to almost lanceolate (distinctly cordate in *M. dilatatum*). Comparisons of leaf shape between species must be made between leaves taken from similar positions on the aerial stem, because leaf shape also varies along the length of a single shoot (see FIGURE 3). This precaution is particularly important with regard to the dimerous species since the two cauline leaves they bear are quite different from one another.

The leaf vasculature is similar to that of many other genera of tribe Polygonatae (Conover, 1982). A large median vein divides the leaf into equal halves, and each half is again divided by a vein of lesser strength. The four resulting panels are likewise equally divided and subdivided by ever finer parallel veins until panel widths of 0.8–2 mm are attained. Very fine commissural bundles then tie the parallel veins together. I term the pattern of venation in which adjacent parallel veins are of very different diameters as “veins ranked.” This pattern differs from that shown by *Maianthemum stellatum*, *M. paludicolum*, and *M. trifolium*, in which adjacent parallel bundles are more nearly equal in strength, giving the leaves a striate appearance. This difference is the only taxonomic character associated with leaf venation. The reticulate venation found in the related genus *Prosartes* D. Don is not seen here, and distinctions based on three, five, or seven “main veins” are not tenable.

Hairs and denticles occur on the leaf, as well as on the main stem and the inflorescence axes. Hairs are always unicellular, pliable, and 80–300 μm long. Denticles protrude in two rows along each margin, most often near the apex. They may extend down the margin of the leaf to the base, sometimes also occurring along the veins on the abaxial surface and along the ribs of the stem and inflorescence. Denticles are approximately 20–80 μm long and are rounded or pointed, with the point directed outward or apically. The hairs and denticles in *Maianthemum* are no different from those found in other genera in the Polygonatae. Some previous authors (Butters, 1927; Fassett, 1935; Okuyama, 1935) have employed these fine features to distinguish taxa, usually at the

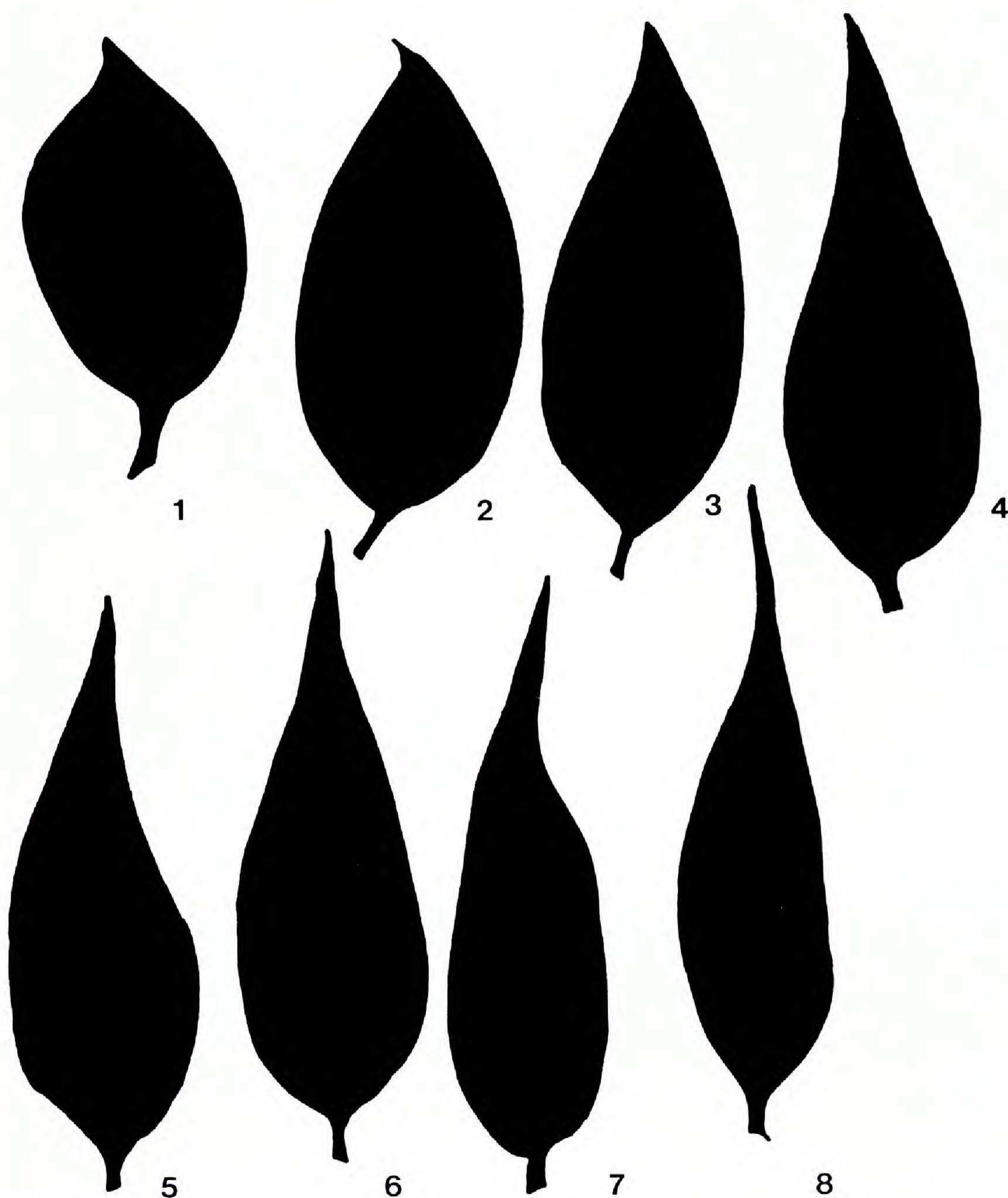


FIGURE 3. Leaf silhouettes from single stem of *Maianthemum septifolium* (LaFrankie 84-V-19C, GH), numbered from base toward apex.

varietal level, but I have not found them to be useful taxonomic criteria. Some species, such as the epiphytes *M. amoenum* and *M. macrophyllum*, which are glabrous and highly polished on all surfaces, are quite constant in these features. However, species such as *M. scilloideum* and *M. racemosum*, which typically have an indumentum, also include some totally glabrous individuals, as well as many others with intermediate levels of hairiness. My observations on both *Maianthemum* and other genera in the Polygonatae indicate that the presence or absence of these simple unicellular hairs is generally much too variable to justify the retention of forms or varieties based on this criterion alone.

INFLORESCENCE

The branching pattern in the inflorescence is the most useful feature by which to recognize species of *Maianthemum*, and I classify the inflorescences among four basic types. Three of these—panicles (main axis bearing lateral racemes at the nodes), complex racemes (main axis with two to seven flowers clustered at each node), simple racemes (main axis with a single flower at each node) (see FIGURE 4)—are found in New World species. The fourth type, found only in some Asian species (e.g., *M. henryi* (Baker) LaFrankie), consists of a main axis with flowers clustered at some nodes and fully extended racemes at one or two lower nodes.

Two fundamental and somewhat unusual features associated with lateral branches in the inflorescence are the apparent absence of both a basal prophyll (the first foliar element is a bract subtending a pedicel) and a terminal flower (the branch is morphologically indeterminate). These features are most clear in the large paniculate species, and less so in species with smaller, condensed inflorescences.

Analysis of the inflorescence is facilitated by locating the persistent bract that subtends every lateral axis. The bracts are usually small and scarious but are sometimes (as in the type specimen of *Smilacina racemosa* f. *foliosa* Marie-Vict., a synonym of *Maianthemum racemosum*) as large as small foliage leaves. Alternatively, the uppermost foliage leaf may be reduced to a small bract, thus giving the inflorescence a long peduncle, as in the type specimen of *S. racemosa* var. *cylindrata* Fern. (a synonym of *M. racemosum*).

Bracts associated with pedicels vary in position among the different species and can be a key feature in identifying herbarium specimens. In general, one bract subtends each pedicel (this is termed “basal” or “subtending”), but in *Maianthemum amoenum* it occurs at midlength along the pedicel. In *M. trifolium*, which has a simple raceme, each pedicel is subtended by one bract and may bear an additional bract either at its base or at its midpoint.

The evolutionary relationships among the different types of inflorescences may be complicated by both reduction and elaboration of the lateral racemes. One relationship that is rather clear at present is between some of the species with panicles and some with compound racemes. The inflorescences of many species (e.g., *Maianthemum scilloideum* and *M. septifolium*) are similar in miniature form within the resting buds, although they may differ in the number of flowers per node. As the leafy shoot expands, the lateral axes of the inflorescence may extend through uninterrupted meristematic growth as elongated racemes (as in *M. septifolium*) or remain compressed as dense fascicles (as in *M. scilloideum*). Even within a normally paniculate species such as *M. racemosum*, lateral axes sometimes fail to elongate, resulting in dense, columnar inflorescences. Such variants appear occasionally in *M. racemosum* throughout the United States and are especially common in Colorado.

One unusual feature of the panicle in *Maianthemum* is that the first one or two flowers on a lateral raceme are usually inserted directly at the base of the raceme. This position is attained because the internode below the pedicel fails to elongate, thereby isolating the first flower. Although the significance of this feature is uncertain, its constancy among many species is readily apparent.

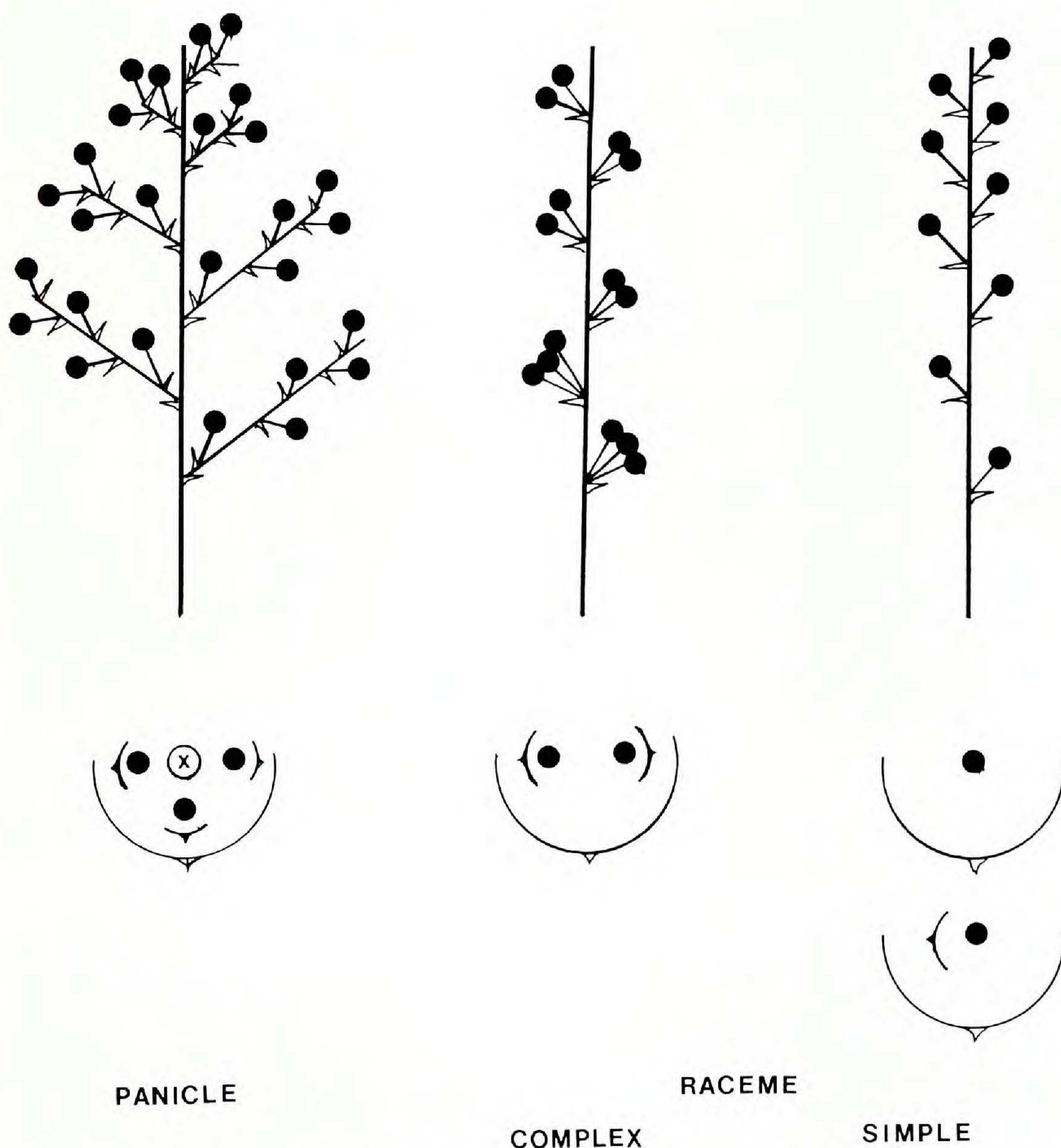


FIGURE 4. Schematic illustration of inflorescence architecture in New World species of *Maianthemum*. Lines = main axes, lateral axes, and pedicels; dots = flowers. Main and lateral axes indeterminate; prophyll lacking; all flowers subtended by bract; lateral axes usually arranged in helix but shown as distichous for clarity. Three types shown, with general view above, transverse view of individual lateral axis below: left, panicle with lateral axes racemes; center, complex raceme with lateral axes fascicles; right, simple raceme with lateral axes single flowers, sometimes with additional bract at base or near midpoint.

FLOWER

The flowers of *Maianthemum* are relatively small and inconspicuous and are characteristic of the lily family. They may be trimerous (six tepals, six stamens, three carpels) or dimerous (four tepals, four stamens, two carpels) through reduction (Utech & Kawano, 1976), but otherwise the flowers of different species are roughly similar to one another, differing chiefly in color, dimensions of parts, and disposition of tepals.

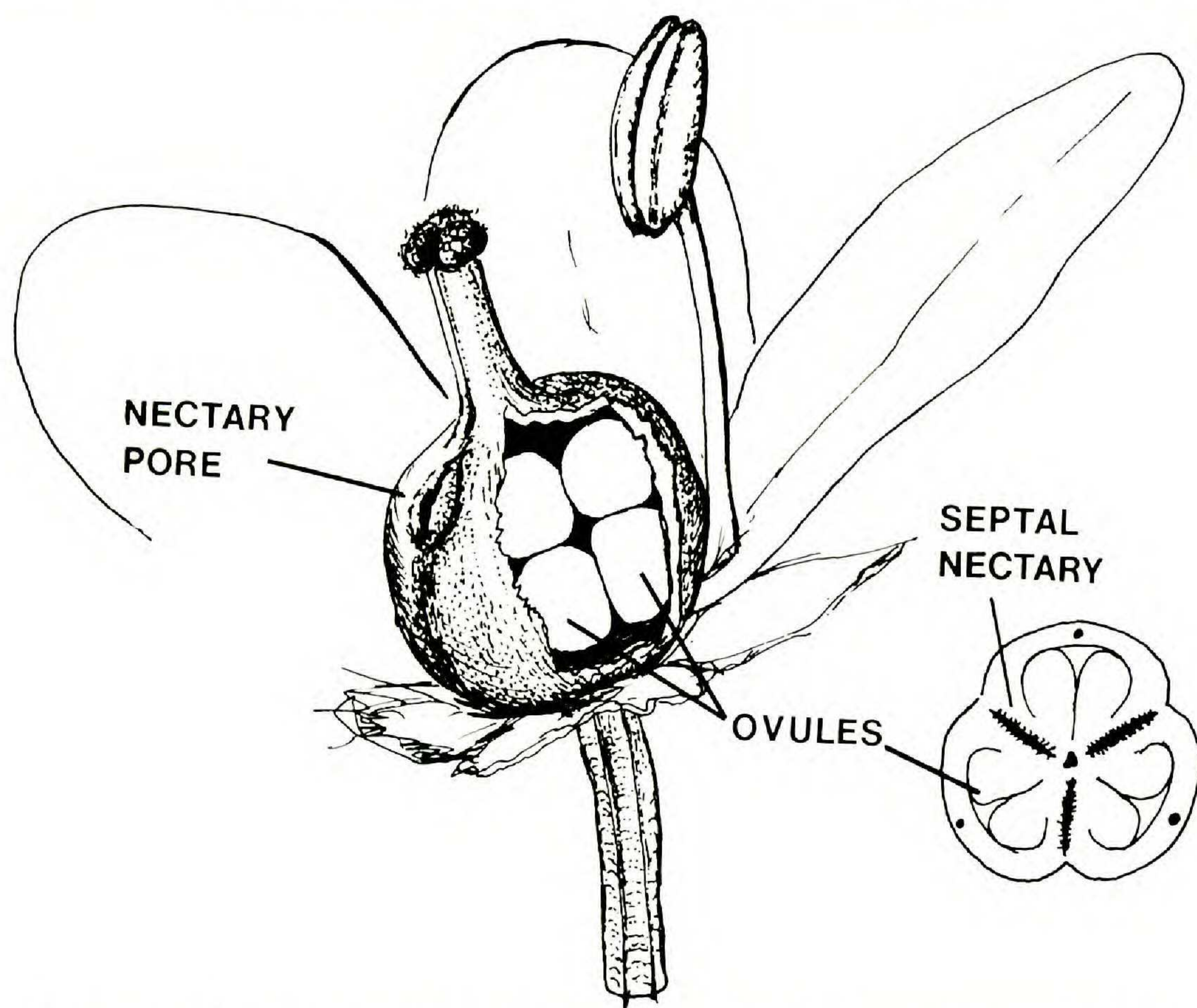


FIGURE 5. Floral morphology in New World species of *Maianthemum*: tepals free, more or less 2-ranked; stamens inserted near tepal base; nectary cells surrounding septal cavity; nectary pore with prominent lip; carpels with 1, 2, or 4 ovules.

The basic form of the flower is illustrated in FIGURE 5. The tepals are almost always uniform and are inconspicuously two-ranked. Among the New World species the tepals are always free, with the perianth spreading, reflexed, or cupuliform; in some Asian species such as *Maianthemum henryi*, the perianth is campanulate. The stamens are inserted at the base of the tepals or up to 1 mm above (as in *M. flexuosum*). The anthers are mostly cylindrical, tetralocular, and longitudinally dehiscent. According to Takahashi and Sohma (1983), the pollen of all New World species of *Maianthemum* is ca. 45 μm long, monocolpate, and with a reticulate exine.

The ovary varies in shape from spherical to cylindrical; the two or three carpels are weakly fused, and each has a single locule. The number of ovules in each carpel varies among the species from one to four but is most commonly two. All species have anatomically identical septal nectaries, although the prominence of the nectary pore varies, as does the volume of nectar exuded. In most species the exuded nectar is inconspicuous, but in *Maianthemum septifolium* the volume is so great that three very large drops accumulate at the junction of the three septal grooves and the adjacent stamens. The style is usually less than 0.5 mm wide and about as long as the ovary; the stigma is generally lobed and a little wider than the style. Seeds are more or less spherical, although in

some species with 12 seeds per fruit (e.g., *M. macrophyllum*), the seeds are conical with one or more flattened faces.

Seed diameter differs significantly among species but is not reliable in herbarium material because drying reduces the diameter from 20 to 40 percent. The seeds of all species are structurally uniform. The testa is thin and papery, straw colored or light brown. The endosperm is white, scaly, and rich in food reserves that are stored in the greatly enlarged cell walls. The embryo is always small and straight; the cotyledon can be spherical or claviform.

Most species of *Maianthemum* have snow-white flowers, but some have flowers infused with green or yellow, and others have them with flecks of red-violet. A few of the Central American species are more variable in flower color (including rose or lavender), but I have rejected the varietal ranking that Emons (1945) gave these individuals because color can vary through a whole range of shades even on a single plant.

CYTOLOGY

Chromosome number and morphology are uniform in most species studied to date (Therman, 1956; Kawano & Iltis, 1966; Kawano, Ihara, Suzuki, & Iltis, 1967; Valentine & Hassan, 1971; Sen, 1974). The haploid chromosome number is 18: one long (ca. 10 μm) with a metacentric constriction; nine medium-length, of which two have metacentric constrictions and seven have acentric or subterminal constrictions; and eight small (ca. 5 μm) with more or less metacentric constrictions. A few species show various levels of intraspecific polyploidy, but in general, evolution within this genus has been unaccompanied by gross chromosomal change.

ECOLOGY AND DISTRIBUTION

Most species of *Maianthemum* are forest herbs, but there are many exceptions, reflecting the broad ecological amplitude of the genus with regard to water, temperature, and light. For example, *M. stellatum* grows on sand dunes, *M. trifolium* and *M. paludicolum* occur in sphagnum bogs in full sun, and *M. amoenum* is found only as an epiphyte in the canopy of cloud forests.

Most of the species require cool temperatures and abundant moisture. In Central America *Maianthemum* grows in locations above 1500 m altitude that receive more than 1500 mm annual rainfall. The genus is generally hardy within these limits, and at least one species seems to be found in most of the areas where these two conditions are met.

Some of the ecological aspects of growth habit are mentioned above. Growth is generally episodic, with the phenological cycle closely tied to the seasons. The forest herbs of the Temperate Zone emerge in early spring, extending their foliage leaves before the forest canopy develops and then persisting through the remainder of the summer in light to moderate shade. In most of the tropical species, new shoots are extended between January and June, which coincides with the drier part of the year. This perhaps allows for more reliable pollination but also requires that water and nutrients be reserved within the rhizome. This constraint would apply all the more to the epiphytic species.

Little is known concerning the pollination biology of *Maianthemum*. My own observations indicate that the North American species are visited by a wide variety of small bees, flies, and beetles. The floral morphology of the tropical species also suggests general insect pollination, but two species may have specialized pollinators. The yellow-green flowers of the epiphyte *M. macrophyllum* are cupulate and open very slowly over a period of several weeks. The flowers of the terrestrial herb *M. flexuosum* are relatively large and usually lavender in color. The individual flowers are comparatively conspicuous (other species of *Maianthemum* gain their conspicuousness through aggregation of many tightly packed flowers in the inflorescence).

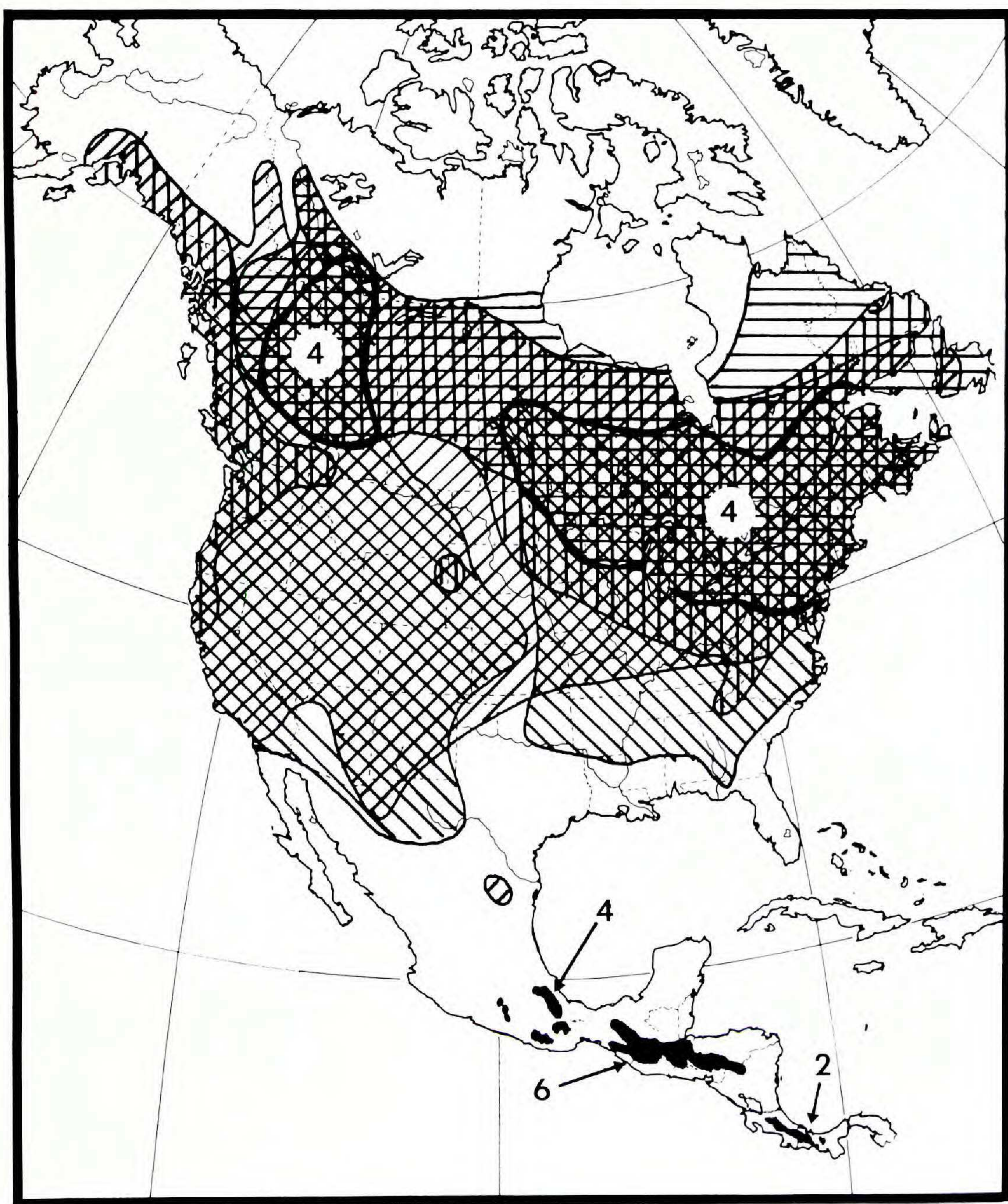
The breeding system in *Maianthemum* is also unknown. Two Asian species of *Maianthemum* (*M. hondoense* (Ohwi) LaFrankie and *M. yezoense* (Franchet & Savat.) LaFrankie) are reported to be dioecious, but their breeding systems have never been verified in the field (Kawano, pers. comm.). All species in the New World bear perfect flowers, but whether or not cross-pollination is required is not known.

In general, the species of *Maianthemum* are distinct and easily recognized. The four species in eastern Canada, for example, show absolutely no intergradation; they are thoroughly distinct, could never be confused, and evidently never hybridize in the wild. The species of Central America are relatively constant in the more critical morphological features, but they tend to be much more variable than the North American ones in leaf color, texture, and indumentum, as well as in other minor features. This may be due in part to the isolated and discontinuous population structure of species in the region, brought about by the highly dissected topography.

As mentioned in the introduction, the continental distribution of the genus (see MAP 1) shows a major discontinuity between the Rio Grande and the state of Mexico, with centers of specific diversity in Guatemala (6 species) and eastern and western Canada (4 species)—a truly remarkable disjunction. Whereas many related genera (such as *Clintonia* Raf.) show Asian-American disjunctions, and others such as *Streptopus* Rich. extend southward to the Asian tropics, *Maianthemum* is the only genus of tribe Polygonatae to be represented in the Neotropics.

The distribution of *Maianthemum* within Central America conforms to the general pattern exhibited by other montane taxa. It is bounded to the north by the arid regions of central Mexico and to the south by the lowlands of eastern Panama. Between these boundaries it has three centers of concentration: Veracruz-Oaxaca, Chiapas-Guatemala, and Costa Rica-Panama. These regions are separated from one another by the relatively broad expanses of the Isthmus of Tehuantepec and the lowlands of southeastern Nicaragua.

Maianthemum shares a pattern of distribution with those genera of the North Temperate Zone that have representative species in the tropical mountains, but there has been little work on just how these species came to occupy a tropical environment. In particular, the time of introduction of the northern elements into the tropical mountains remains a source of debate. The suggestion by Deevey (1949) that the North Temperate taxa arrived during the Pleistocene in response to glacial advance has been much criticized (Braun, 1955; Martin & Harrell, 1957; Graham, 1973). Earlier, Braun (1950, p. 486) had suggested



MAP 1. Centers of taxonomic diversity for New World species of *Maianthemum*. Distribution of species plotted in overlapping series and number of sympatric species indicated, demonstrating broad disjunction between north temperate and tropical montane species.

that, "The warmth of the Eocene and Oligocene epochs may have resulted in withdrawal of temperate forms to high elevations, in eastern United States and in Mexico. During the Pliocene, a climatic barrier—the dryness of the Plains—developed. Even if withdrawal to higher elevations was accomplished earlier, a final separation would have been effected by the climatically dry belt, and contemporaneously with the late Tertiary shrinkage of mesophytic floras." An early date of immigration (pre-Miocene) into Central America would help explain the parallels between species of Old World and New. New World species

would be polyphyletic and would represent several successive periods of immigration from Asia, the first (Central American species) occurring in the early Cenozoic, and the last (boreal species) during the Neogene.

Studies by Miranda and Sharp (1950) and Steyermark (1950) have emphasized that genera found in both the North Temperate Zone and the Central American mountains are of two biogeographic types. One group consists of closely related species pairs or varieties; *Liquidambar* L. is an example often cited. The other group comprises species endemic to Guatemala and southern Mexico with nearest relatives in the western United States and eastern Asia; oaks are mentioned as examples of this type. *Maianthemum* falls more readily into the latter group; the species of Central America with large panicles, spherical rhizomes, and axillary lateral buds share more features with some species of Japan and China than they do with those of eastern Canada. However, the Asian species should be carefully studied in the field before any significant conclusions concerning their phylogenetic relationships are reached.

METHODS AND SPECIMEN CITATION

Specimens at A, BR, CAN, CAS, CR, DS, DUKE, F, GH, GOET, K, LL, MEXU, MICH, MO, MSC, NEBC, NY, ORE, PH, TENN, TEX, TRT, UC, US, WAT, WIS, WS, WTU, and XAL were annotated during the course of this study. Additionally, photocopies or single specimens were examined from DAO, FI, FTG, KNK, LSUS, MT, and WVA.

Species descriptions are arranged alphabetically; they are based on the examination of approximately 6000 North American and 1400 Central American specimens. Additionally, I was able to collect and cultivate living specimens of all taxa except *Maianthemum dilatatum*, *M. gigas* var. *crassipes*, *M. racemosum* subsp. *amplexicaule*, and *M. salvinii*. Additional materials of rhizomes and flowers were preserved in FAA for study in the laboratory.

The infraspecific taxa I recognize are in accordance with generally accepted definitions. They are morphologically distinct from one another and represent either geographically well-defined variants (ranking of subspecies), or scattered, isolated, or sympatric variants (ranking of varieties).

I have omitted specimen citations from the account of the North American species except in the case of type specimens, or to document limits of geographic distribution. A complete list of annotated specimens for the Central American species is provided. These are arranged geographically, from northwest to southeast. Duplicates are arranged alphabetically.

Distribution maps for the North American species, which are well known and have a continental distribution, were handled somewhat differently than those for the Central American ones, some of which are new and are more narrowly distributed. For the North American species I plotted the distribution upon an arbitrarily positioned grid in which each unit is 40 km on a side. Many western and Canadian specimens that are located only to county or province must be rejected by this method, but the resulting maps are uniform in meaning. Published distribution records, which are reliable and based on herbarium specimens, are included in the description but are not placed on the maps. References for the county distribution maps include Deam (1940); Steyermark

(1963); Braun (1967); Radford, Ahles, and Bell (1968); Voss (1972); Barkley (1977); Harvill, Stevens, and Ware (1977); Mohlenbrock and Ladd (1978); and Wherry, Fogg, and Wahl (1979). Within Central America specific collection sites are plotted only when they can be located precisely (i.e., when the site can be confidently located beneath the map symbol used to denote the taxon).

TAXONOMY

Maianthemum G. Weber ex Wigg. Prim. Fl. Hols. **14**: 29. 1780, nomen conserv.

TYPE SPECIES: *M. convallarium* Wigg., nomen illegit. (= *Convallaria bifolia* L., *M. bifolium* (L.) F. W. Schmidt).

Unifolium Ludwig, Inst. Regn. Veg. ed. 2. 124. 1757, nomen rejic. TYPE SPECIES: *U. bifolium* (L.) E. Greene (= *Convallaria bifolia* L.).

Vagnera Adanson, Fam. Pl. **2**: 496. 1763, nomen rejic. TYPE SPECIES: *V. stellata* (L.) Morong (= *Convallaria stellata* L.).

Valentinia Heister ex Fabr. Enum. ed. 2. 37. 1763, nomen illegit. (incl. type of *Unifolium* Ludwig, 1757, nomen rejic.).

Polygonastrum Moench, Methodus, 637. 1794, nomen rejic. TYPE SPECIES: *P. racemosum* (L.) Moench (= *Convallaria racemosa* L.).

Sciophila Wibel, Prim. Fl. Werth. 147. 1799. TYPE SPECIES: *S. convallarioides* Wibel, nomen illegit. (= *Convallaria bifolia* L.).

Smilacina Desf. Ann. Mus. Natl. Hist. Nat. **9**: 51. 1807, nomen conserv. TYPE SPECIES: *S. stellata* (L.) Desf. (= *Convallaria stellata* L.).

Styrandra Raf. Amer. Monthly Mag. Crit. & Rev. **2**: 266. 1818. TYPE SPECIES: *S. bifolia* (L.) Raf. (= *Convallaria bifolia* L.).

Sigillaria Raf. *ibid.* **3**: 100. 1818 (= *Smilacina* Desf.).

Asteranthemum Kunth, Abh. Königl. Akad. Wiss. Berlin **1848**: 33. 1850. TYPE SPECIES: *A. vulgare* Kunth, nomen illegit. (= *Convallaria stellata* L.).

Medora Kunth, *ibid.* 34. TYPE SPECIES: *M. divaricata* Kunth, nomen illegit. (= *Smilacina fusca* Wallich).

Jocaste Kunth, Enum. Pl. **5**: 154. 1850. TYPE SPECIES: *J. purpurea* (Wallich) Kunth (= *Smilacina purpurea* Wallich).

Maia Salisb. Gen. Pl. 64. 1866. TYPE SPECIES: *Convallaria bifolia* L.

Neolexis Salisb. *ibid.* TYPE SPECIES: *Convallaria racemosa* L.

Tovaria Necker ex Baker, J. Linn. Soc., Bot. **14**: 564. 1875, non Ruiz & Pavón, 1794. TYPE SPECIES: *T. racemosa* (L.) Baker (= *Convallaria racemosa* L.).

Oligobotrya Baker, Hook. Icon. Pl. **16**: 1537. 1886. TYPE SPECIES: *O. henryi* Baker.

Terrestrial, aquatic, or epiphytic herbs, 10 cm to 2.5 m tall. Rhizome fleshy, persistent, densely clumped with units subspherical, or spreading with units filiform. Leafy stem pendent, leaning, or upright, with 2 to 17 foliage leaves distichously arranged. Leaves simple, clasping or with short petiole (or, in some dimerous-flowered species, long petiole); blade usually ovate, the base rounded, the apex acute to caudate, the margin flat or undulate, denticulate or not, the surfaces glabrous or pubescent. Inflorescence terminal, a panicle or raceme, with 15 to 400 flowers, lateral branches or fascicles distichous or in helix. Flowers usually perfect (some Asian species reportedly dioecious), trimerous or dimerous; pedicel usually subtended by bract; perianth spreading, cupuliform, or campanulate; tepals usually uniform, ovate, obovate, or triangular, 0.5–1.1 mm long, usually white (also lavender to red, or green); stamens inserted

at tepal base, the anther tetralocular, introrse; ovary with 2 or 3 carpels, septal walls with nectaries, the style usually less than 1.5 mm long, the stigma 2- or 3-lobed, usually less than 1 mm broad. Fruits usually lobed, 4–12 mm broad, with 1 to 12 seeds; seeds usually spherical, 3–6 mm in diameter, with thin, pale brown testa and scaly endosperm. Chromosome number $2n = 36$ most commonly reported.

KEY TO THE NEW WORLD SPECIES OF MAIANTHEMUM

1. Inflorescence a panicle.
 2. Lateral inflorescence axes > 2 cm long, spreading or slightly ascending; pedicels usually perpendicular to lateral axis, with bract subtending, longest pedicel < 7 mm; perianth spreading.
 3. Rhizome epidermis replaced by corky periderm; tepals conspicuous, > 2 mm long; Meso-America.
 4. Rhizome fleshy, cylindrical to subspherical, < 10 cm long, plagiotropic; foliage leaves with veins ranked in strength; terrestrial or epiphytic.
 5. Rhizome > 1.5 cm broad; leafy stem > 1 m long; foliage leaves 12 to 18.
 6. Plant 1.5–2.5 m tall; individual rhizome units broad-claviform to subspherical, 3–5 cm in diameter; inflorescence dense, with flowers inserted on lateral axes at 3–4(–10) mm intervals. . . . 5. *M. gigas*.
 6. Plant 1–1.5 m tall; individual rhizome units short-cylindrical to narrow-claviform, 2–4 cm in diameter; inflorescence diffuse, open, with flowers inserted on lateral axes at intervals of (7–)10–20 mm. 9. *M. paniculatum*.
 5. Rhizome < 1.5 cm broad; leafy stem < 1 m long; foliage leaves 6 to 8 (to 10). 13. *M. septifolium*.
 4. Rhizome woody, narrow-cylindrical, much elongated, > 20 cm long, upright; foliage leaves with veins of uniform strength; in alpine bogs. 8. *M. paludicolum*.
 3. Rhizome epidermis persistent, yellow-brown, waxy; tepals inconspicuous, 0.5–1 mm long; North America. 10. *M. racemosum*.
 2. Lateral inflorescence axes < 2 cm long, sharply ascending; pedicels drawn toward main inflorescence axis, the bract not subtending, usually located near midpoint of pedicel; longest pedicel > 15 mm; perianth cupuliform; Meso-America.
 7. Inflorescence upright, 4–6(–9) cm long; fruit subspherical, 5–8 mm broad. 1. *M. amoenum*.
 7. Inflorescence pendent, 15–20 cm long; fruit 3-lobed, 10–12 mm broad. 7. *M. monteverdense*.
1. Inflorescence a simple or complex raceme.
 8. Individual rhizome units cylindrical, 1–30 cm by 1–2 mm; roots restricted to nodes; epidermis persistent, waxy; floral shoot with 2 to 4 foliage leaves; North America.
 9. Base of cauline leaf with narrow or broad sinus; inflorescence a complex raceme, 1 to 3 flowers per node; flowers dimerous.
 10. Plant 10–25 cm tall; upper cauline leaf ovate, sessile, the base with narrow sinus; lower cauline leaf cordate, with petiole 1–7 mm long; flowers 1 to 3 (usually 2) per node. 2. *M. canadense*.
 10. Plant 20–45 cm tall; upper cauline leaf triangular to cordate, with short petiole, the base with broad open sinus; lower cauline leaf deeply cordate, with petiole 7–10 cm long; flowers 1 to 4 (usually 3) per node. 3. *M. dilatatum*.

9. Base of cauline leaf tapered; inflorescence a simple raceme; flowers trimerous. 15. *M. trifolium*.
8. Individual rhizome units cylindrical to claviform, 3–50 cm by 5–30 mm; roots at nodes and internodes; epidermis not persistent; floral shoot with 6 to 11 foliage leaves.
 11. Vegetative surfaces glabrous, polished; perianth cupuliform; epiphytic; Meso-America.
 12. Inflorescence upright or arched upward; pedicels stiff, reflexed, 4–9 mm long. 6. *M. macrophyllum*.
 12. Inflorescence pendent; pedicels spreading or drooping, 15–20(–30) mm long. 11. *M. salvinii*.
 11. Vegetative surfaces glabrous or pubescent, not polished; perianth spreading; terrestrial.
 13. Individual rhizome units with internodes uniformly extended; roots uniform; inflorescence a complex raceme; Meso-America.
 14. Inflorescence upright, main axis straight or slightly flexuous; longest pedicel 3–4.5 mm long; fruits usually spherical. 12. *M. scilloideum*.
 14. Inflorescence pendent, main axis strongly flexuous; longest pedicel 8–21 mm long; fruits strongly 3-lobed. 4. *M. flexuosum*.
 13. Individual rhizome units with 2nd and 3rd internodes greatly extended; roots dimorphic; inflorescence a simple raceme; North America. 14. *M. stellatum*.

1. ***Maianthemum amoenum*** (H. L. Wendl.) LaFrankie, *Taxon* **35**: 588. 1986.
FIGURE 6, MAP 2.

Smilacina amoena H. L. Wendl. *Allg. Gartenzeitung* **18**: 137. 1850. TYPE: Guatemala, Totonicapán, road between Los Encuentros and Totonicapán, 3100 m, 1 April 1977, D. Smith & Clancy 553 (neotype, here chosen, F!).

Epiphytic herb, 0.5–0.8 m tall. Roots uniform, 8 to 12 per rhizome unit, evenly scattered, 20–60 cm by 1.2–1.8 mm. Rhizome densely clumped, the individual units subspherical, 3–5 cm broad, the scale leaves 6 or 7, the internodes 2–3 mm long, the lateral buds 4, axillary, 1 or 2 developing leafy shoots; epidermis replaced by periderm; starch present only near rhizome apex. Leafy stem leaning or upright, 25–40 cm long, 5–9 mm broad at base, the surface smooth, polished; foliage leaves 6 to 9 (to 11); internodes 2–5 cm long, shorter apically. Leaves clasping (some Mexican specimens with petiole 2 mm long); blade ovate, 6–13 by 2.5–5.5 cm, the apex acute or short-acuminate, the base rounded, the margin flat, denticles inconspicuous and appressed, the veins ranked, the surfaces glabrous, polished. Inflorescence a panicle (sometimes appearing subpaniculate when immature) with 25 to 75 flowers; main axis upright, stiff, straight, 4–6(–9) cm long, 1.5–2.5 mm broad at base, smooth, flattened, red, or white to pink with red patches, glabrous; internodes 1.5–4 mm long (lower ones 1–10 mm); lateral branches arranged in helix, sharply ascending, spreading as flowers bloom, each 1–2 cm long with 3 to 5 flowers, of which 1 inserted at branch base and others at ca. 4 mm intervals. Flowers trimerous; pedicel 12–20 by 0.7–1 mm, weakly ribbed or smooth, with bract inserted between base and midpoint; perianth cupuliform, the tepals uniform, 3.5–6.5 by 1.5–2.5 mm, lavender, or white infused with pink; stamens inserted

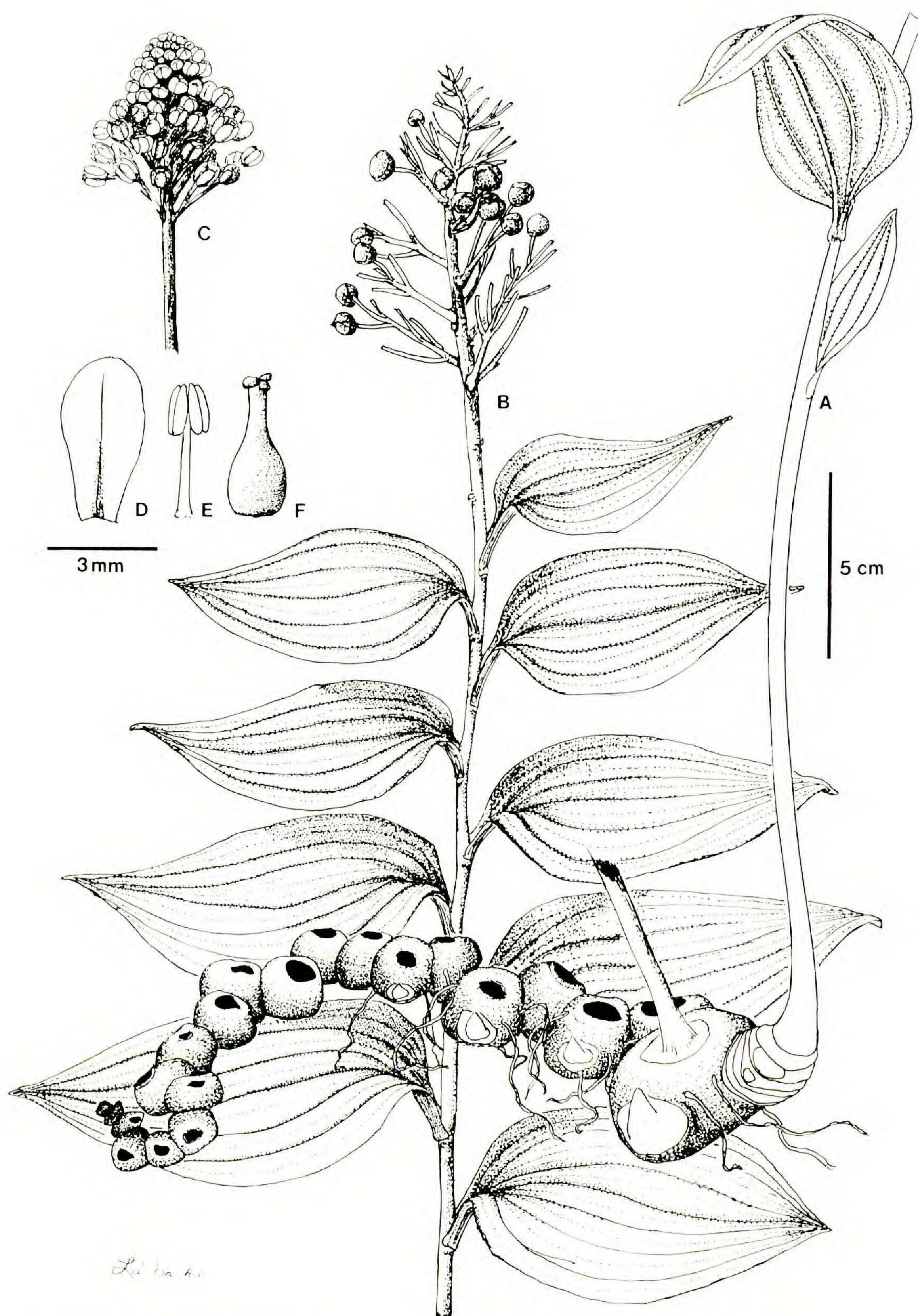
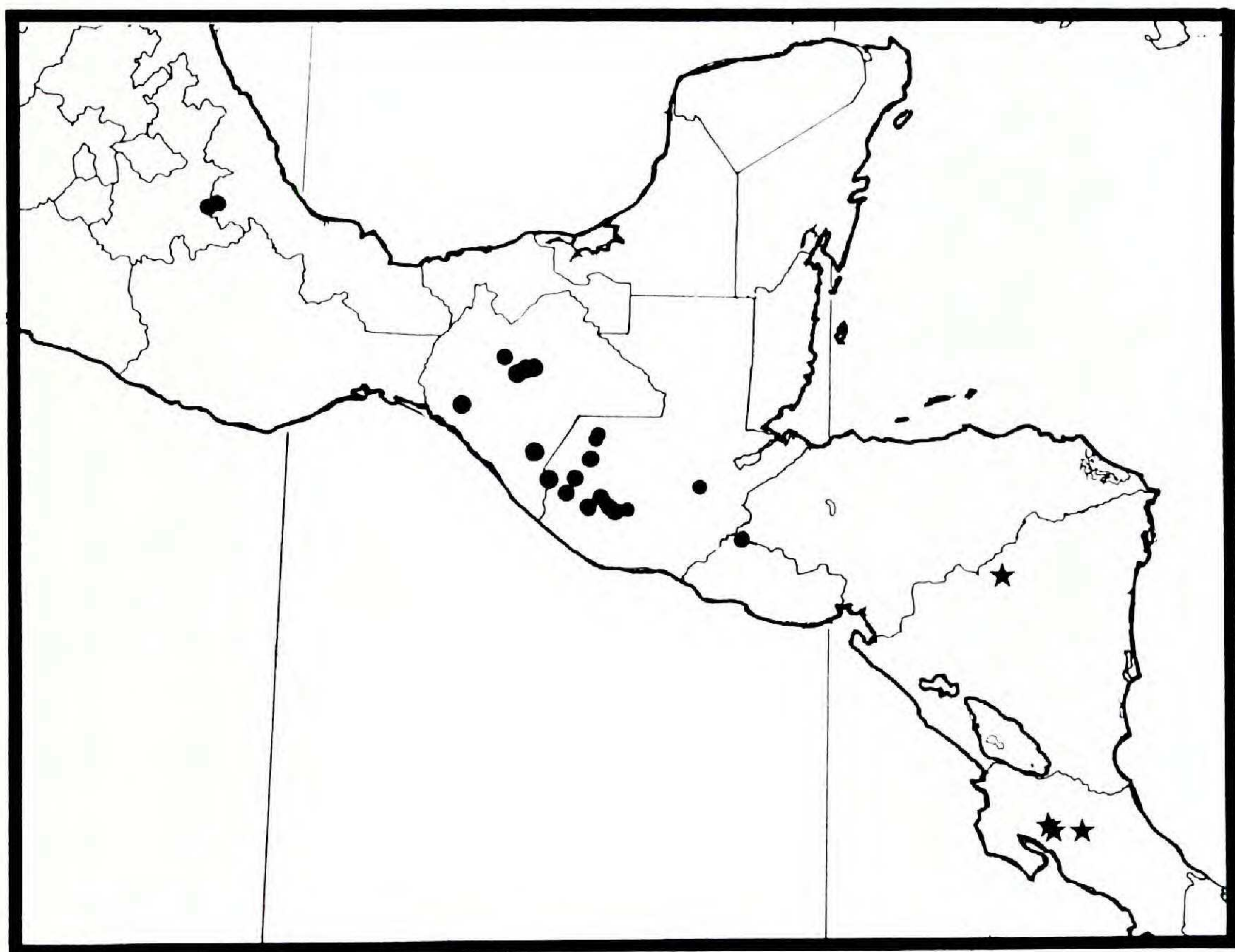


FIGURE 6. *Maianthemum amoenum*: A, rhizome and lower portion of leafy shoot; B, upper portion of leafy shoot and infructescence; C, inflorescence; D, tepal; E, stamen; F, ovary. (A, B based on *LaFrankie 84-V-21A*, GH; C-F on *Standley 61123*, F.)



MAP 2. Distribution of *Maianthemum amoenum* (dots) and *M. monteverdense* (stars).

at tepal base, the filament 1.5–2 mm long, thin, the anther 0.5–0.8 mm long; ovary spherical to cylindrical, 1–1.5 by 1 mm, the style 1–1.5 mm long, the stigma distinctly 3-lobed, ca. 0.7 mm broad. Fruits spherical to weakly 3-lobed, 5–8 mm broad, green when young, maturing to red; seeds up to 12, slightly flattened, 3–4 by 2–3 mm. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Occasional; epiphytic at height of 5–15 m or more above ground, although sometimes persisting in blowdowns; often in dense clumps covering *Quercus*, *Drimys*, and other canopy trees of cloud forest; 2300–3300 m alt. New shoots developing annually; flowering January–April; fruits retained through October.

Northern limit in Veracruz; occasional in northern highlands of Chiapas, Sierra Madre del Sur, and Cerro Tres Picos, east through Guatemala (where somewhat more common); rare in El Salvador.

SPECIMENS EXAMINED. **Mexico.** VERACRUZ: Nogales, 1500 m, *Matuda* 1154 (GH, MICH, MO, US); Acultzingo, *Ugent* 2372 (WIS). CHIAPAS: vic. Tenejapa, *Ton* 889 (DS, LL, NY); El Triunfo, *Xolocotzi* x-456 (MEXU); Pueblo Nuevo Solistahuacán, *Zuill* 586 (DS); Cerro Hueytepec, *Alexander* 1218 (MICH, NY), *Breedlove* 26256 (DS, MO), *Carlson* 1681 (F), *Laughlin* 136 (DS, LL), 1026 (DS, F, US); Cerro Zontehuitz, 9300 ft, *Breedlove* 9588 (DS), 14522 (DS, LL, WIS); Cerro Mozotal, *Breedlove* 22723 (DS); SE side Cerro Tres Picos [in Sierra Madre del Sur], *Breedlove* 34417 (DS); Malé-Motozintla, *R. Hernandez* 398 (MEXU); Siltepec, *Matuda* 15268 (F, MEXU). **Guatemala.** HUEHUETENANGO: vic. San Mateo Ixtatán, *Breedlove* 8929 (DS), 8939 (F); Paquix, Alto Cuchumatanes, *Holdridge* 2291 (US). QUICHÉ:

no further location, *Aguilar 1228* (F). QUEZALTENANGO: SE of Palestina, *Standley 84303* (F); Volcán Zunil, *Steyermark 34685* (F); 31 mi E of Quezaltenango, *S. White 5409* (MICH). TOTONICAPÁN: Cumbre del Aire, *Hunnewell 17108* (GH); between Los Encuentros and María Tecún, *Molina 15942* (F); between Los Encuentros and Totonicapán, *D. N. Smith 553* (F). SOLOLÁ: Volcán Santa Clara, *Steyermark 46876* (F). SAN MARCOS: above San Marcos, *Bunting 346A* (DUKE, NY, US); Volcán Tajumulco, *Plowman 3040* (GH), *3049* (LL); between Sibinal and Cajula, *Steyermark 36024* (F). CHIMALTENANGO: Caldera, *J. Johnston 1109* (F); vic. Tecpán, *Collin 21* (US), *Hunnewell 14654* (GH), *J. Johnston 633* (F), *Skutch 232* (US), *Standley 61123* (F). EL PROGRESO: between Finca Piamonte and Volcán Santa Luisa, *Steyermark 43553* (F). **El Salvador.** SANTA ANA: E slope La Esesmile, *Tucker 1033* (F, LL, MICH, NY, PH, UC, US).

A neotype of *Maianthemum amoenum* is required because I can find no specimen of the single cultivated plant used by H. L. Wendland in writing his description. The plant was collected in Guatemala, and its rhizome was sent to Göttingen with a shipment of orchids in 1845; most likely no specimen was made. While searching for an appropriate neotype, I located two specimens collected in Costa Rica by Wendland's son in 1857, seven years after the publication of *Smilacina amoena*. The annotations differ in the spelling of the location, one citing Volcán Berba, the other Volcán Yerba. They were probably both from Volcán Barba (Heredia Province). The younger Wendland was in Göttingen for several years just prior to leaving for Costa Rica, and he probably saw the plant described by his father. It is also quite likely that his father examined the Costa Rican specimens of *Maianthemum* and perhaps even compared them with the cultivated plant. Therefore, one would think these specimens should give a good impression of the plant H. L. Wendland described.

Unfortunately, these two specimens are quite different from the species to which the name *Maianthemum amoenum* has conventionally been applied. When H. L. Wendland's description (there was no illustration) is compared with these Costa Rican specimens, it is clear that the younger Wendland erred in his annotation and that the Costa Rican material does not belong to the species his father described. There are several key disagreements between the protologue and the specimens. According to the description, the leaves are somewhat clasping and have polished surfaces; the lateral racemes of the inflorescence bear four or five flowers with pedicels up to 18 mm long, drawn together in an upward-arching array. In the specimens from Costa Rica, the leaves are glabrous but not polished, and they have distinct petioles 4–5 mm long; the lateral racemes of the inflorescence are spreading, with pedicels 6–6.5 mm long and usually perpendicular to the lateral axis. Accordingly, I have annotated the Wendland specimens *M. gigas* and have chosen a modern representative specimen to serve as the neotype.

An unusual feature of *Maianthemum amoenum* is the great number of raphide crystal sacs that develop in the rhizome. In most species of *Maianthemum*, such sacs are a conspicuous cell type but are never very numerous. However, here they are a dominant feature of the histology. Each sac has a large vacuole that contains a bundle of unusually minute raphide crystals. Additionally, each vacuole is filled with mucilage and surrounded by a hard outer shell that stains red-brown in IKI (and is thus presumably proteinaceous or a polysaccharide).

The gradual depletion of the stained matter in the older portions of the rhizome suggests that it is a storage product.

2. **Maianthemum canadense** Desf. Ann. Mus. Natl. Hist. Nat. **9**: 54. 1807.

FIGURE 7A–G, MAP 3.

Smilacina canadensis (Desf.) Pursh, Fl. Amer. Sept. **1**: 233. 1814; *Unifolium canadense* (Desf.) E. Greene, Bull. Torrey Bot. Club **15**: 287. 1888; *Maianthemum bifolium* (L.) F. W. Schmidt f. *canadense* (Desf.) Farw. Bull. Torrey Bot. Club **42**: 356. 1915. TYPE: not determined.

Smilacina canadensis (Desf.) Pursh var. *ovalis* Pursh, Fl. Amer. Sept. **1**: 233. 1814; *Unifolium bifolium* (L.) E. Greene f. *ovale* (Pursh) Farw. Bull. Torrey Bot. Club **42**: 356. 1915; *Maianthemum canadense* Desf. var. *ovale* (Pursh) Butters, Minnesota Stud. Pl. Sci. **4**: 437. 1927. TYPE: not determined.

Smilacina canadensis (Desf.) Pursh var. *trifolia* Pursh, Fl. Amer. Sept. **1**: 233. 1814; *Unifolium bifolium* (L.) E. Greene var. *trifolium* (Pursh) Farw. Bull. Torrey Bot. Club **42**: 356. 1915. TYPE: not determined.

Styrandra amplexicaulis Raf. Autik. Bot. 68. 1840. TYPE: United States, Allegheny Mtns., *Rafinesque s.n.* (holotype, PH?, probably destroyed; lectotype, here chosen, protologue).

Maianthemum canadense Desf. var. *interius* Fern. Rhodora **16**: 211. 1914; *Unifolium canadense* (Desf.) E. Greene var. *interius* (Fern.) House, Bull. New York State Mus. **254**: 224. 1924; *Maianthemum canadense* Desf. subsp. *interius* (Fern.) Löve & Löve, Bull. Torrey Bot. Club **81**: 33. 1954. TYPE: United States, South Dakota, Piedmont and Little Elk Creek, 4000 ft, 27 June 1892, *Rydberg 1043* (holotype, GH!; isotype, US!).

Maianthemum canadense Desf. var. *carolinianum* Butters, Minnesota Stud. Pl. Sci. **4**: 437. 1927. TYPE: United States, North Carolina, moist woods near Highlands, 31 May 1897, "Biltmore Herbarium" no. 16b (holotype, MINN; isotypes, GH!, PH!, US!).

Maianthemum canadense Desf. var. *pubescens* Gates & Ehlers, Pap. Michigan Acad. Sci. **32**: 30. 1948. TYPE: United States, Michigan, Emmet or Cheboygan Co., *Gates & Ehlers s.n.* (holotype, not located; MICH?).

Maianthemum canadense Desf. f. *oswaldii* Mold. Phytologia **5**: 84. 1954. TYPE: United States, New Jersey, Bergen Co., Alpine, *Oswald s.n.* (holotype, NY).

Terrestrial forest herb, 10–25 cm tall. Roots uniform, occurring only at scale-leaf nodes, 2 to 6 per node, 8–15 cm by 0.5–1 mm. Rhizome an irregularly branched sympodium, the individual units cylindrical, 2–30 cm by 1–1.5 mm, the scale leaves 3 to 10, the internodes 0.5–5 cm long, shorter apically, the lateral buds 1 at every node, axillary, 1 to 4 forming renewal shoots; epidermis persistent; starch deposited throughout, depleted in older portions. Leafy stem upright, 10–18 cm long, 1.5–2.5 mm broad at base, the surface smooth, usually glabrous in plants of eastern North America and slightly pubescent in plants of upper Midwest; foliage leaves 2 or 3 (or 4); internodes 1.5–2.5 cm long. Upper leaf sessile, lower one(s) sessile or with petiole to 7 mm long; blade ovate to subcordate, 4.5–7(–9) by 3–4.5(–5.5) cm, the apex acute, or short-caudate (1–2 mm), the base rounded, with narrow, shallow sinus and basal lobes 2–5 mm long, the margin flat, denticles distinct, the veins ranked in strength. Inflorescence a complex raceme with 12 to 25 flowers; main axis stiff, arching upward, slightly flexuous, 3–4.5 cm long, 1–1.5 mm broad at base, round or flattened, most often smooth, green, glabrous or slightly pubescent;

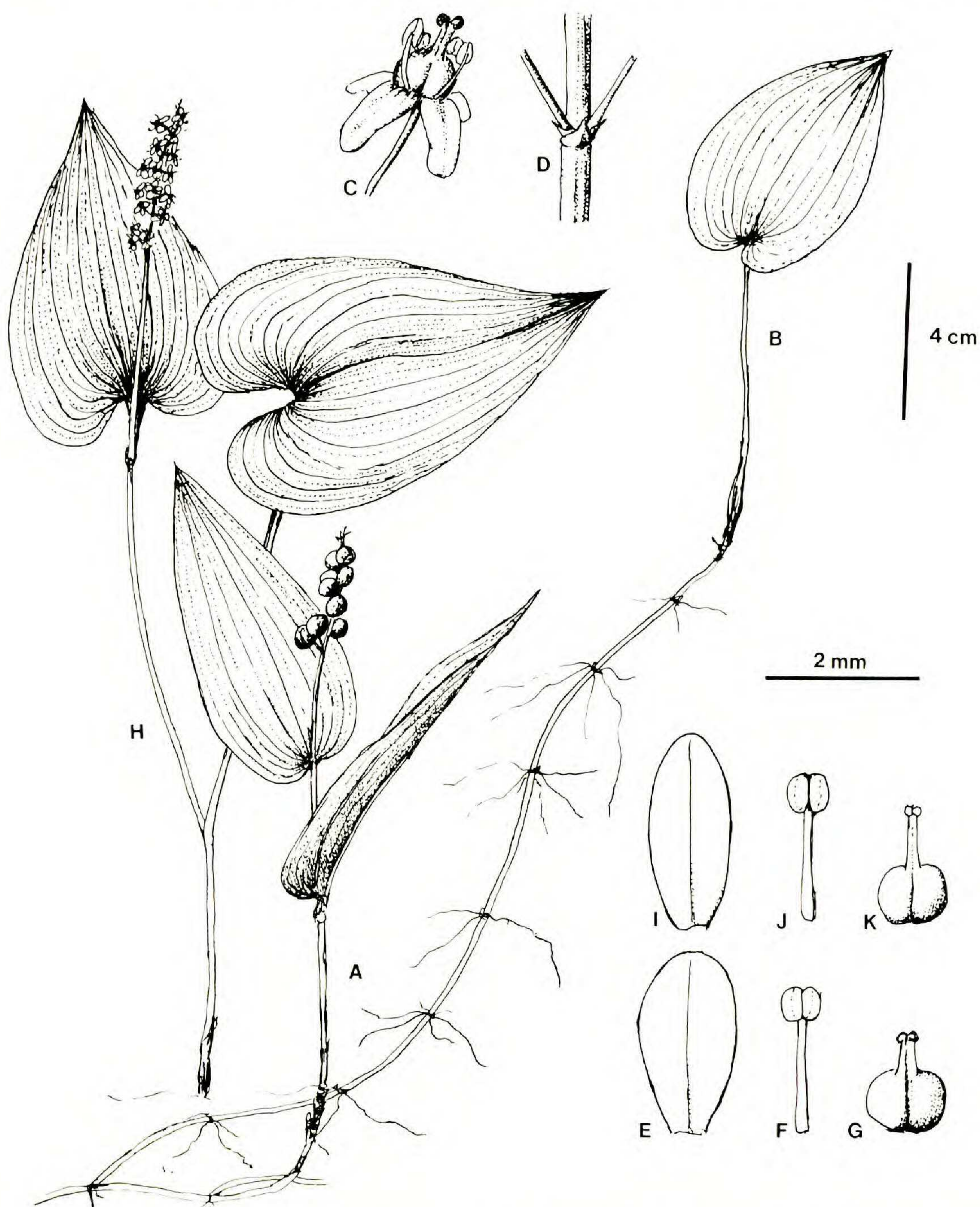
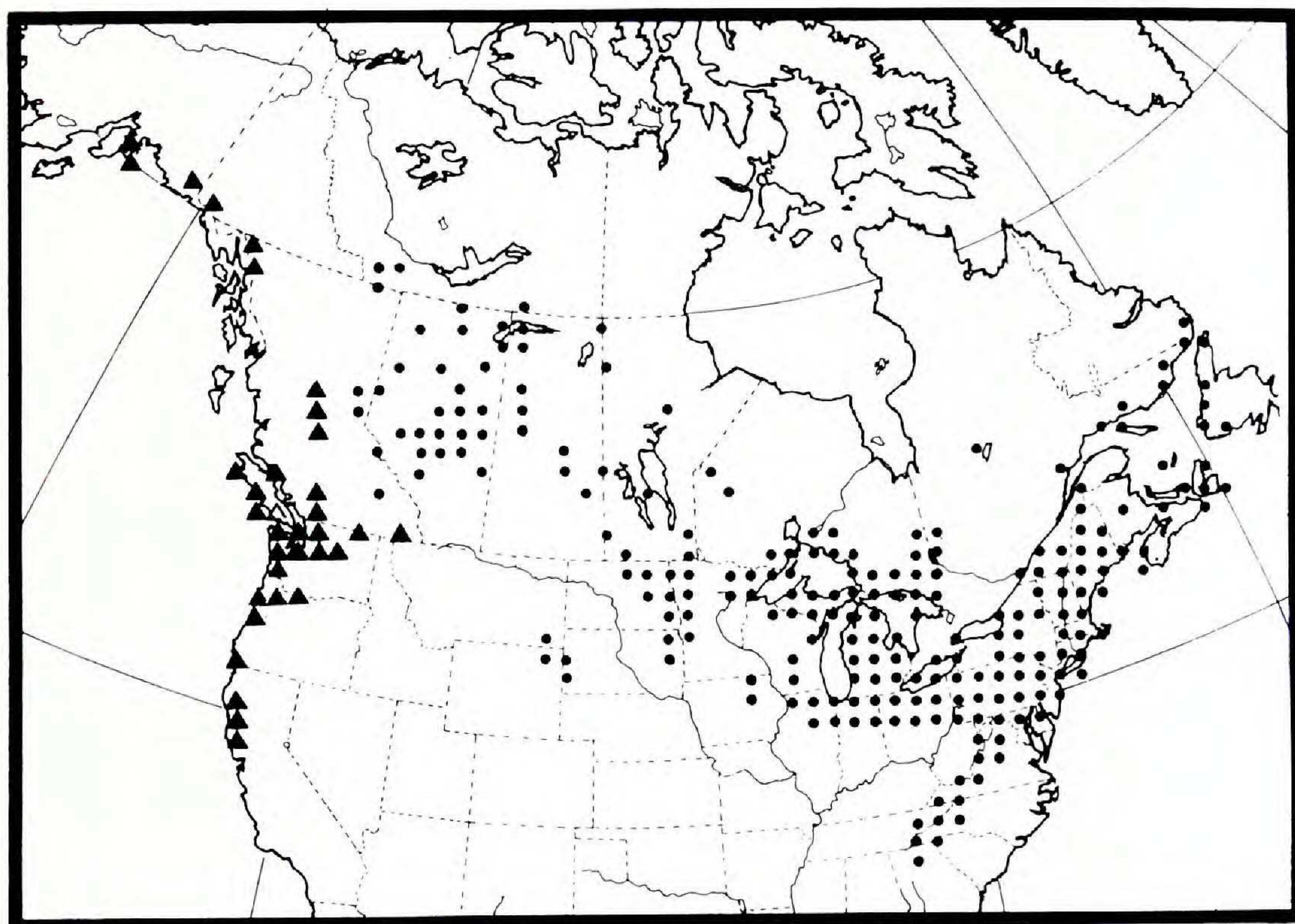


FIGURE 7. A–G, *Maianthemum canadense* (LaFrankie 78, GH): A, habit of bifoliate reproductive shoot; B, habit of unifoliate vegetative shoot; C, flower; D, inflorescence node with 2 pedicels, each subtended by bract, entire fascicle subtended by bract; E, tepal; F, stamen; G, gynoecium. H–K, *M. dilatatum* (Taylor 1552, GH): H, habit of bifoliate reproductive shoot, with long-petiolate cauline leaf; I, tepal; J, stamen; K, gynoecium.

internodes 6 to 12, 1–3 mm long; fascicles arranged in helix, with 1 to 3 (usually 2) flowers at each node, spreading, with bract subtending each fascicle. Flowers dimerous; pedicel 3–7 by 0.2–0.5 mm, ribbed, glabrous, with bract subtending; tepals uniform, weakly 2-ranked, reflexed, 1.5–2 by 0.8–1 mm, white; stamens



MAP 3. Distribution of *Maianthemum canadense* (dots) and *M. dilatatum* (triangles).

inserted at tepal base, the filament 1–1.5 mm long, very thin, the anther 0.2–0.4 mm long; ovary spherical, 0.8–1 mm broad, the style 0.5–0.8 mm long, the stigma distinctly 2-lobed, 0.3–0.5 mm broad. Fruits spherical, 4–6 mm in diameter, green mottled with red when young, maturing to deep translucent red; seeds up to 2, spherical, ca. 3 mm in diameter. Chromosome number $2n = 36, 54, 72$ (Kawano, Ihara, Suzuki, & Iltis, 1967; Valentine & Hassan, 1971).

ECOLOGY AND DISTRIBUTION. Abundant in northern forests (nearly ubiquitous in forests of eastern Canada and the northeastern United States); sea level to 1800 m alt. Flowering May–June; fruits retained through August or September.

From Labrador (Battle Harbor, *Williamson s.n.* (GH, PH)) and Prince Edward Island (Queens Co., *Fernald 7199* (GH, PH)) south along Atlantic coast to New Jersey (Cape May Co., Cape May Courthouse, *Long 7219* (GH, PH)) and Delaware (Newcastle Co., Red Clay Creek, *Long 30211* (GH, PH)), then inland at higher elevations as far south as Virginia (Roanoke Co., McAfee Knob, *C. Wood 6055* (GH)) and North Carolina (Transylvania Co., Lake Logan, *Hardin 715* (GH)). West of Appalachians, southern limit much to north, extending across northern Indiana (LaPorte Co., W end of Hudson Lake, *Friesner 21408* (GH)); and Jefferson Co. (Deam, 1940)) and Illinois (LaSalle Co., Starved Rock, *Greenman s.n.* (GH)), with outlying location in Henry Co., Missouri, *fide* Barkley (1977), although unreported there by Steyermark (1963). Northern limit extending from central Québec (Lac Mistassini, *Rousseau 2005* (GH)) through Ontario (Sandy Lake, *Moir 4065* (GH)), where nearly ubiquitous in coniferous forests although not widely collected, and to Northwest as far as Alberta (Wood

Buffalo Park, *Raup 2025* (GH)) and British Columbia (E of Bouchie Lake, *Calder 18170* (GH); 1.5 mi S of Prince George, *Calder 12341* (GH)). Western limit chiefly determined by southern and northern ones (species absent from Rockies south of Canada, despite slightly disjunct occurrence in Black Hills of South Dakota—no location, *Cutler 2623* (GH)).

The North American plants of *Maianthemum* with dimerous flowers were placed under *M. bifolium* until Desfontaines (1807) described them as the separate species *M. canadense*. I have not determined a lectotype for this species because I have not examined Desfontaines's herbarium, which was transferred to FI. A specimen of the material he studied may still be there. The specimens studied by Pursh are not at PH or any other American herbarium but may be at OXF.

The six varietal names published for this species are based on insignificant differences, and I have placed them all in synonymy. The limitation of pubescence as a varietal character is discussed under the general heading of leaf morphology. Butters (1927) claimed that the distinction between the plants of the upper Midwest and those of the East was based on vegetative features as well as pubescence. However, his data do not indicate any discrete and consistent difference between eastern and western plants; they merely demonstrate the extent to which minor vegetative differences occur within this otherwise broadly uniform species.

The three dimerous species of *Maianthemum* are very similar to one another in every important feature, and as a group, they have a continuous circumboreal distribution. Although they differ only in minor aspects of leaf shape, they have been recognized as separate species because these differences are rather constant and the species are found within relatively well-defined geographic borders. *Maianthemum canadense* is found in eastern and central North America; the upper cauline leaf is ovate to elliptic and has a very narrow basal sinus. *Maianthemum bifolium* is Eurasian in distribution; the upper cauline leaf is nearly triangular, and it has a moderately broad basal sinus. *Maianthemum dilatatum* is restricted to the Pacific coast of North America, with a limited extension to the Kamchatka peninsula and northern Japan; the upper cauline leaf is more nearly cordate, with a broad basal sinus, and the plant is nearly twice as large as that of the other two species (see FIGURE 8). In general, there is no point of sympatry or intergradation between *M. canadense* and *M. bifolium*; likewise, *M. canadense* and *M. dilatatum* are allopatric and quite distinct. However, both *M. dilatatum* and *M. bifolium* grow in eastern Asia, and considerable intergradation between the species occurs there.

The overall similarity between the three dimerous species, and the intergradation of species in eastern Asia, has led to some controversy over their proper taxonomic status. Kawano and colleagues (Kawano, Ihara, & Suzuki, 1968a, 1968b; Kawano & Suzuki, 1971; Kawano, Suzuki, & Koyima, 1971) found that the three dimerous species have a uniform karyotype, an overlapping range of morphological variation, and a relatively similar ecology but nonetheless concluded that there is "... reasonable certainty [the three species] are recognizable as specifically distinct entities." In light of their generally uniform vegetative and floral forms, I am inclined toward the opinion of Engler (1888)

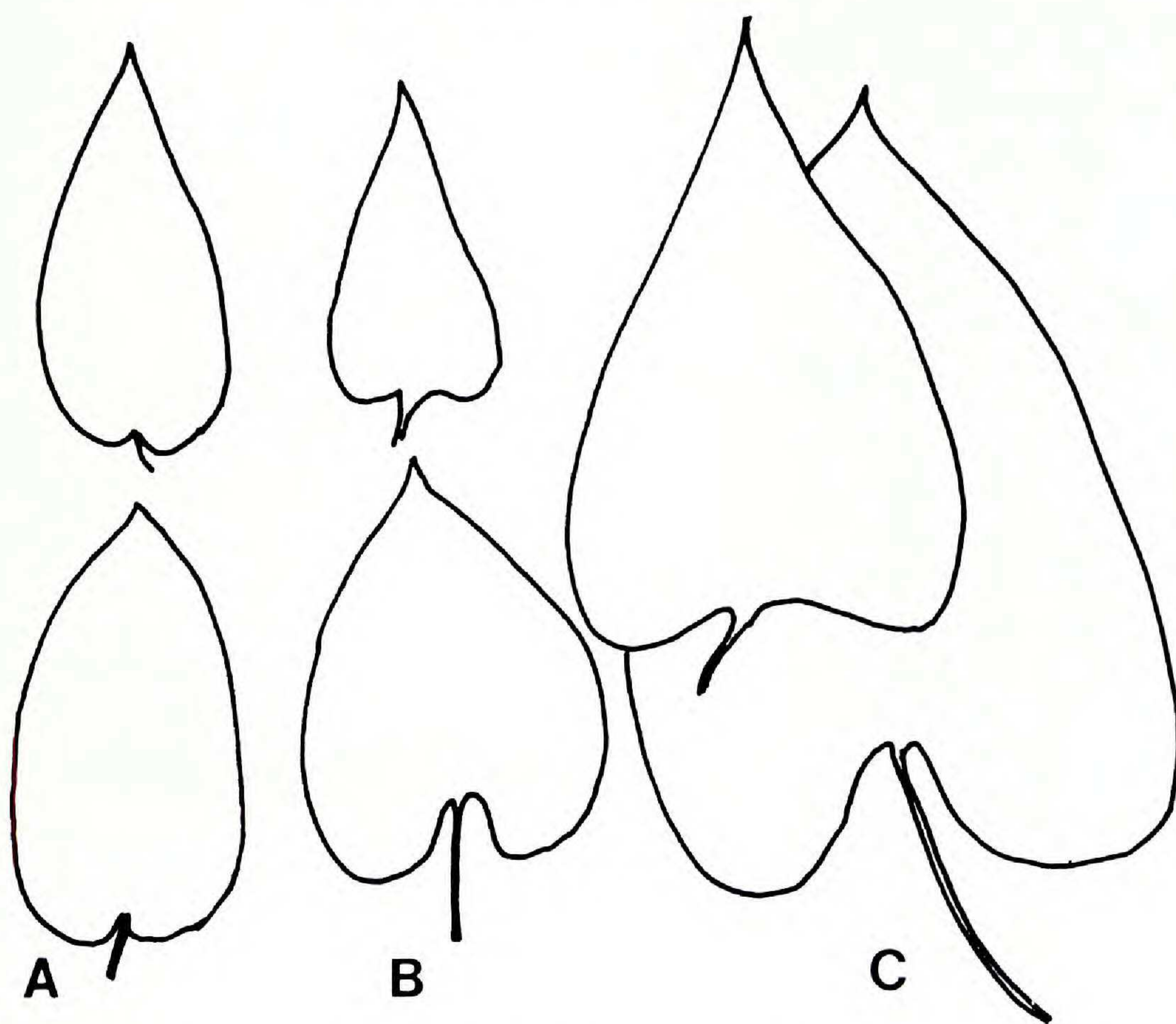


FIGURE 8. Leaf shape in 3 species of *Maianthemum* with dimerous flowers (upper cauline leaf above, lower cauline leaf below): A, *M. canadense*; B, *M. bifolium*; C, *M. dilatatum*.

and Farwell (1915) that a single species—circumboreal in distribution, and consisting of three distinct subspecies—should be recognized. However, because little is known of the interfertility of these species, and because I have not seen *Maianthemum dilatatum* or *M. bifolium* in the field, I continue to follow the conventional treatment and recognize the three species as distinct.

3. ***Maianthemum dilatatum*** (Alph. Wood) Nelson & Macbr. Bot. Gaz. (Crawfordsville) **61**: 30. 1916. FIGURE 7H–K, MAP 3.

Maianthemum bifolium (L.) F. W. Schmidt var. *dilatatum* Alph. Wood, Proc. Acad. Nat. Sci. Philadelphia **1868**: 174. 1868; *Smilacina dilatata* Nutt. ex Alph. Wood, *ibid.*, pro syn.; *Smilacina dilatata* Nutt. ex Baker, J. Linn. Soc., Bot. **14**: 563, 564. 1875, pro syn.; *Unifolium dilatatum* E. Greene, Man. Bot. San Francisco, 316. 1894 (with Nuttall in parentheses). TYPE: United States, [Washington,] “Columbia Woods,” [ca. 1835,] Nuttall s.n. (lectotype, here chosen, PH!; isoelectotype, GH!).

Convallaria bifolia L. var. *kamtschatica* Cham. Linnaea **6**: 587. 1831; *Smilacina bifolia* (L.) Pursh var. *kamtschatica* (Cham.) Ledeb. Fl. Ross. **4**: 127. 1853; *Maianthemum bifolium* (L.) F. W. Schmidt var. *kamtschaticum* (Cham.) Trautv. & Meyer, Fl. Ochot. **1**: 474. 1856; *Unifolium bifolium* (L.) E. Greene var. *kamtschaticum* (Cham.) Piper, Contr. U. S. Natl. Herb. **11**: 200. 1906; *Maianthemum kamtschaticum* (Cham.)

V. Komarov, *Puteshestvie na Kamchatku*, 451. 1909, nomen nudum, reprinted in "V. L. Komarov: Izbrannye Sochineniia" 6: 451; *Maianthemum bifolium* var. *kamtschaticum* (Cham.) Jepson, *Fl. W. Calif.* 109. 1911; *Unifolium kamtschaticum* (Cham.) Gorman, *Muhlenbergia* 2: 376. 1916; *Maianthemum kamtschaticum* (Cham.) Nakai, *Bot. Mag. (Tokyo)* 31: 282. 1917; *Maianthemum canadense* Desf. var. *kamtschaticum* (Cham.) Kudo, *J. Coll. Agric. Tohoku Imp. Univ.* 11: 92. 1922; *Maianthemum dilatatum* (Alph. Wood) Nelson & Macbr. var. *kamtschaticum* (Cham.) Butters, *Minnesota Stud. Pl. Sci.* 1: 443. 1927; *Maianthemum bifolium* subsp. *kamtschaticum* (Cham.) E. Murray, *Kalmia* 12: 22. 1982. TYPE: U.S.S.R., Kamchatka peninsula (no specimen cited, probably at LE).

Maianthemum intermedium Vorosch. *Bjull. Glavn. Bot. Sada* 38: 50. 1960. TYPE: U.S.S.R., Regio Primorsky, Vladivostok, prope Okeanskaja, in sylvis, 7 Sept. 1950, *Woroschilov s.n.* (MHA).

Terrestrial forest herb, to 45 cm tall. Roots uniform, occurring only at scale-leaf nodes, 2 to 6 per node, 8–20 cm by ca. 1 mm. Rhizome an irregularly branched sympodium, the individual units cylindrical, 10–20 cm by 1.5–2.5 mm, the scale leaves 3 to 10, the internodes 1.5–3 cm long, shorter apically, the lateral buds 1 at every node, axillary, 1 to 4 developing as leafy shoots; epidermis persistent; carbohydrate reserves not known. Leafy stem upright, 15–35 cm long, 2–4 mm broad at base, the surface smooth, glabrous; foliage leaves 2 or 3 (or 4); internodes 4–8 cm long. Upper leaf subpetiolate, lower one with petiole (2.7–)4–7(–8) cm long; blade cordate, 6–10 by 5–8 cm, the apex sharply acute, the base lobed, with very deep sinus and lobes 2.5–3.5 cm long, the margin flat, denticles indistinct, the veins ranked. Inflorescence a complex raceme with 15 to 40 flowers; main axis arching upward, slightly flexuous, 3.5–5 cm long, 0.8–1.5 mm broad at base, rounded or flattened, weakly ribbed, green, glabrous; internodes 10 to 18, 1–3 mm long; fascicles arranged in helix, with 1 to 4 (or 5) flowers at each node, spreading, bract subtending each fascicle. Flowers dimerous; pedicel 3–5 by 0.2–0.4 mm, ribbed, glabrous, with bract subtending; tepals uniform, reflexed, 2–3.2 by ca. 1.5 mm, white; stamens inserted at tepal base, the filament 1.5 mm long, very thin, the anther 0.2–0.3 mm long; style 0.4–0.5 mm long, stigma distinctly 2-lobed. Fruits spherical, 4–6 mm in diameter, green with red spots when young, maturing to translucent red; seeds 1 or 2, spherical, 2–3 mm in diameter. Chromosome number $2n = 36$ (Kawano, Ihara, Suzuki, & Iltis, 1967; Kawano & Suzuki, 1971).

ECOLOGY AND DISTRIBUTION. Forming dense patches on floor of coniferous and deciduous forests, most abundant in light gaps and near forest margins; broad ecological latitude with respect to light and soil type (Kawano, Ihara, & Suzuki, 1968a, 1968b); sea level to 800 m alt. Flowering May–June; fruits ripening slowly, retained through September or October.

Species generally of Pacific coast of Northwest, ranging eastward to northern Idaho (Bonner Co., Priest Lake, *Piper* 3685 (GH)) and southward to northern California (Humboldt Co., Bishop Pine Lodge, Trinidad, *Parks* 4289 (GH)). Rather common along Canadian coast as far north as northern British Columbia (Haines Road, Mile 45, *Taylor* 1552 (GH); Queen Charlotte Island, *Dawson s.n.* (GH)); less common along northern Pacific through Alaska (Attu Is., *Wil-*

liams 3180 (GH)), and again relatively more common in Kamchatka and northern Japan.

The name of this species is somewhat controversial. Ingram (1966) claimed that Greene's publication of *Unifolium dilatatum* was independent of Wood's earlier publication of *Maianthemum bifolium* var. *dilatatum*, and since there were no holotypes, he felt that the two names should be lectotypified by different specimens. This is important because Nelson and Macbride based their binomial on Wood's, not on Greene's, epithet. As Ingram noted, if the names of Greene and Wood have different types, then the publication of *M. dilatatum* based on Greene is still necessary, yet would create a later homonym that would, in effect, make *M. kamtschaticum* the correct binomial. However, contrary to Ingram's opinion, there is no reason to believe that the names should be lectotypified by different specimens. Greene was an authority on botanical literature, especially with regard to plants of the western United States, and therefore would surely have been aware of Wood's use of Nuttall's name as a varietal epithet. The fact that Greene chose to place Nuttall's rather than Wood's name in parentheses simply reflects his desire to use the earliest reference for every name. Greene's name is best viewed as simply a new combination in a new ranking of Wood's, and it therefore automatically has the same type as the earlier epithet; in consequence, there is no reason to change the name from the one in common use. The Nuttall specimen from "Columbia Woods" in PH is probably the specimen seen by Wood, or if not, it is a duplicate. In either case it should be the lectotype, not the neotype, as determined by Ingram (1966).

4. ***Maianthemum flexuosum*** (Bertol.) LaFrankie, *Taxon* **35**: 588. 1986.

FIGURE 9, MAP 4.

Smilacina flexuosa Bertol. Nov. Comment. Acad. Sci. Inst. Bononiensis **4**: 411. *t.* 4. 1840 (not Fl. Guatimal. 1840); *Smilacina bertolonii* Kunth, Enum. Pl. **5**: 151. 1850, nomen illegit.; *Tovaria flexuosa* (Bertol.) Baker, J. Linn. Soc., Bot. **14**: 567. 1876; *Vagnera flexuosa* (Bertol.) Standley, J. Wash. Acad. Sci. **15**: 457. 1925. TYPE: Guatemala, ca. 1830, *Velasquez s.n.* (holotype, BOLO, IDC 748. 45: II. 5!).

Smilacina flexuosa Hooker, Icon. Pl. n.s. **2**: *t.* 529. 1843, non Bertol. 1840. TYPE: Guatemala, ca. 1830, *Skinner s.n.* (holotype, K!).

Smilacina flexuosa Bertol. var. *erubescens* Emons, Ann. Missouri Bot. Gard. **32**: 405. 1945. TYPE: Guatemala, San Marcos, between Todos Santos and Finca El Porvenir, 1300–3000 m, 1 March 1940, *Steyermark 36972* (holotype, F!).

Terrestrial forest herb, 0.40–0.75 m tall. Roots uniform, 10 to 18 per rhizome unit, scattered but most numerous at base of leafy shoot, 20–35 cm by 1–1.5 mm. Rhizome a linear sympodium, occasionally forking, the individual units 2–4(–7) by 1–2 cm, slightly flattened, the scale leaves 7 or 8, the internodes 5–8(–20) mm long, shorter apically, the lateral buds 6 or 7, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch deposited in distal portions. Leafy stem arched, 40–70 cm long, 3–4 mm broad at base, the surface slightly ribbed, glabrous; foliage leaves 7 to 9 (to 12); internodes 3.5–6(–10) cm long, shorter apically. Leaves with petiole less than 5 mm long; blade ovate to lanceolate, 8–12 by 3–5 cm, the apex long-acuminate (upper

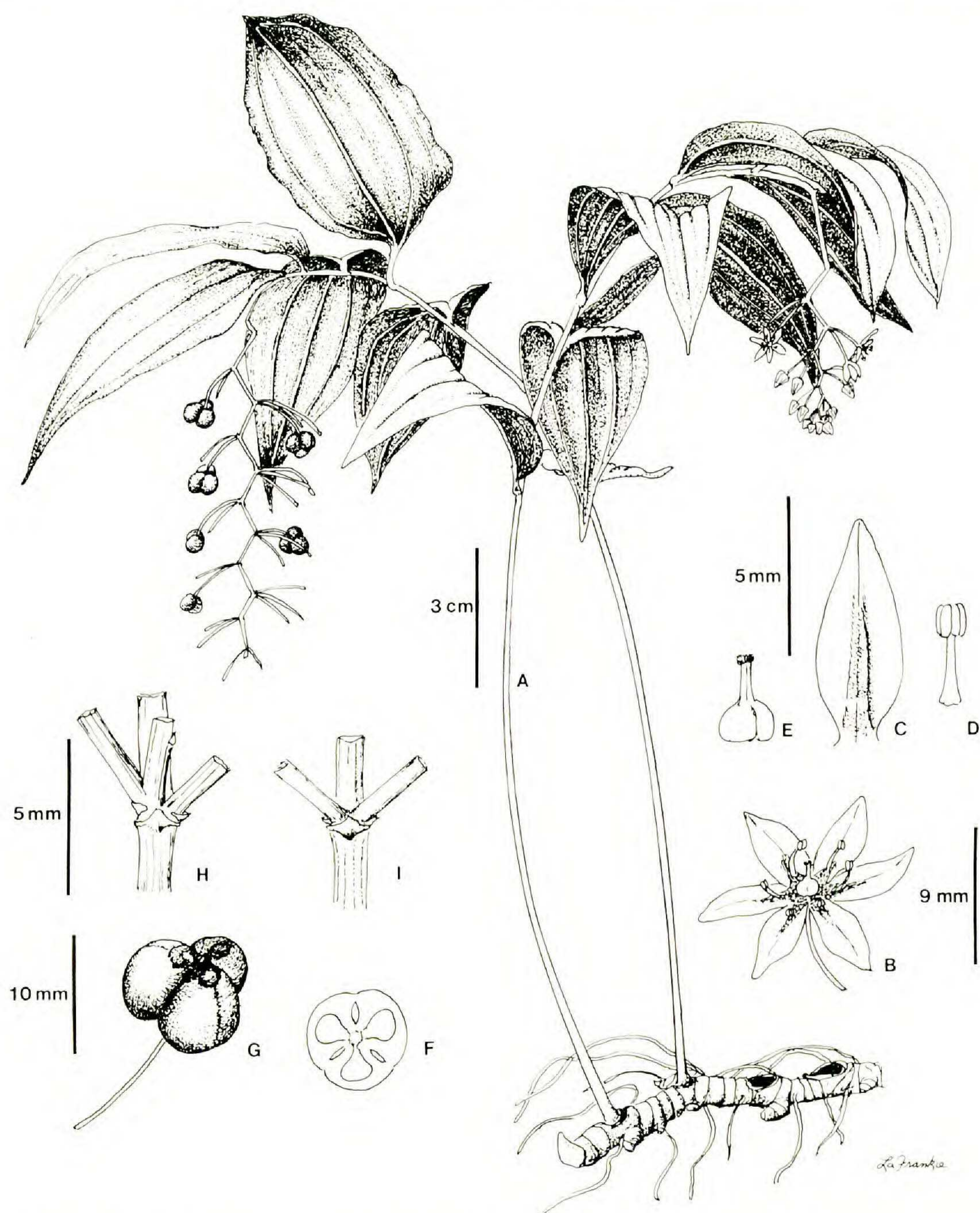
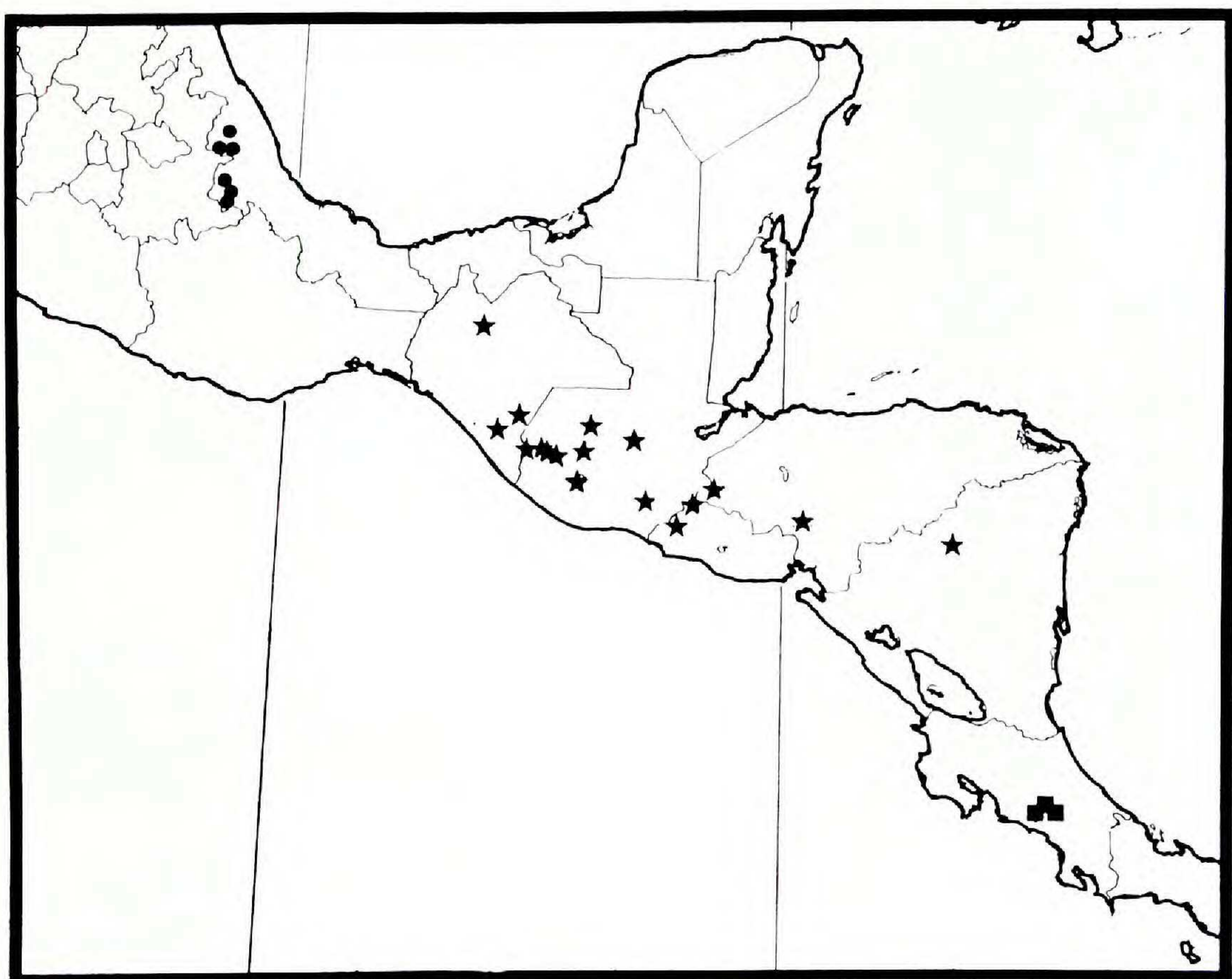


FIGURE 9. *Maianthemum flexuosum* (LaFrankie 84-V-22A, GH): A, rhizome, leafy shoot, both fruit and flowers on same individual; B, flower; C, tepal; D, stamen; E, gynoecium; F, ovary, transverse section, showing 3 locules, 3 cavities of septal nectaries; G, mature fruit; H, I, lateral fascicles.

leaves) or acute to short-acuminate (lower ones), the base rounded to slightly tapered, the margin undulating, entire or rarely denticulate, the veins ranked, the surfaces glabrous, rarely with minute hairs. Inflorescence a complex raceme with 25 to 65 flowers; main axis pendent, flexuous, tapering, 5–18 cm long, 1.5–3 mm broad at base, smooth or slightly ribbed, green, glabrous; internodes 10 to 16, 6–8(–20) mm long; fascicles distichous, with 2 to 4 (to 6) flowers, slightly reflexed and drooping, bract subtending each fascicle. Flowers trimer-



MAP 4. Distribution of *Maianthemum flexuosum* (stars), *M. macrophyllum* (dots), and *M. paludicolum* (squares).

ous; pedicel 8–21(–28) by 0.4–0.6 mm, slightly ribbed, glabrous, with bract subtending (sometimes central pedicel of fascicle with additional bract at mid-length); tepals uniform, spreading to reflexed, 5–11 by 2–3 mm, lavender to pink, rarely white or green-white; stamens epitepalous, 0.5–1 mm above tepal base, the filament narrow-petaloid, 1.5–3 mm long, the anther 0.5–1(–1.5) mm long; ovary spherical to cylindrical, 1 by 1.5–2 mm, the style 1–2 mm long, the stigma 3-lobed, ca. 0.5 mm broad. Fruits distinctly 3-lobed, 7–11 mm broad, green when young, maturing to red; seeds 1 to 3, spherical, 5–6 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Solitary or weakly clonal, in understory of cloud forests; 1450–2200(–2800) m alt. Flowering January–June; fruits set May–August, retained August through following spring; fruiting and flowering stems sometimes overlapping on same individual.

Northwestern limit represented by single specimen from northern highlands of Chiapas, but this location recently cleared. Most common in Sierra Madre del Sur from Chiapas through Guatemala, ranging east to El Salvador; also on scattered mountains in Honduras and Nicaragua.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: vic. Pueblo Nuevo Solistahuacán, *Harrell* 438 (MEXU); Naquivil, vic. Motozintla, *Breedlove* 42749 (DS); Mt. Ovanda, *Matuda* 374 (MEXU, MICH); vic. Escuintla, *Matuda* 4237 (F, GH, LL, MEXU, MO, NY, US); Siltepec, *Matuda* 15266 (DS, F, MEXU); Saxchanal, *Matuda* 17808 (F, MEXU); Chicarras, *E. Nelson* 3762

(US); Cerro del Boquerón, *Purpus* 7415; vic. Volcán Tacaná, *Breedlove* 31634 (DS), *Matuda* 2846 (F, GH, LL, MEXU, MO, US). **Guatemala.** HUEHUETENANGO: Concepción near San Martín, *Seler* 3168 (GH, US); Cerro Pixpíx, Ixtahuacán, *Steiermark* 50561 (F). QUICHÉ: Nebaj, *Heyde* 4647 (GH, K, US). ALTA VERAPAZ: vic. Tactic, *Standley* 90345 (F), *L. O. Williams* 40595 (F, MICH). SAN MARCOS: Volcán Tajumulco, *L. O. Williams* 26881 (F, NY, US); Barranca Eminencia, *Standley* 86507 (F). QUEZALTENANGO: Cantón La Esperanza, 6 km from San Juan Ostuncalco, *Molina* 16647 (F, NY); vic. Volcán Zunil, *Standley* 86027 (F), *L. O. Williams* 22984 (F, NY); above Santa María de Jesús, *Standley* 84859 (F). TOTONICAPÁN: Cerro María Tecúm, *L. O. Williams* 23119 (F). SOLOLÁ: Volcán Santa Clara, *Steiermark* 46885 (F); Volcán San Pedro, *Steiermark* 47227 (F); Volcán Atitlán, *Steiermark* 47382 (F). SUCHITEPÉQUEZ: Volcán Agua, *Kellerman* 7295 (F, NY, US); Volcán Santa Clara, *Steiermark* 46722 (F, NY). CHIMALTENANGO: San Martín, *J. R. Johnston* 1305 (F); Chichavac, *Skutch* 72 (US); Cerro Tecpán, *Standley* 58708 (F); Los Positos above Las Calderas, *Standley* 58708 (F). ESCUINTLA: Volcán Agua, *Almeda* 758 (DUKE), *Uiley* 56 (DUKE), *R. L. Wilbur* 14754 (DUKE). JALAPA: Volcán Jumay, *Steiermark* 32400 (F). SANTA ROSA: Santa Rosa, *Heyde* 3537 (GH, K, NY, US); Zamorora, *Heyde* 4652 (GH, NY, US). ZACAPA: between Loma el Picacho and Cerro de Monos, *Steiermark* 42780 (F, NY). **El Salvador.** SANTA ANA: Montecristo, *Molina* 12522 (F, NY). **Honduras.** INTIBUCÁ: Slone Ardisia, *Molina* 6369 (F, LL). LA PAZ: Sierra Guajiquiro, 5 km from Sabaneta, *Molina* 13896 (F, LL, NY, US). **Nicaragua.** MATAGALPA: Cordillera Dariense, Hacienda Santa María de Ostuma, *Tomlin* 129 (MO); summit of Cerro El Picacho, *D. Stevens* 22166 (MO).

The type specimen of *Maianthemum flexuosum* was recently discovered in BOLO, together with many other Guatemalan types of Bertoloni. Duncan (1983) presented a concise history of the Guatemalan specimens upon which the *Florula Guatimalensis* was based but erroneously concluded that the material had been destroyed during the Second World War. Evidently the specimens were simply misplaced, perhaps after being photographed by IDC for their microfiche edition of the Bertoloni Herbarium. A revised history of the Bertoloni material is now being prepared by the staff at BOLO.

This species is sometimes confused with *Maianthemum scilloideum*, the only other terrestrial species of Central America with a racemose inflorescence, although in their typical forms these species are thoroughly distinct. They are readily distinguished from one another by quantitative differences of the inflorescence (see TABLE) and also by differences in rhizome, floral morphology, and habitat. *Maianthemum scilloideum* is a spreading, clonal herb of high altitudes, typically found in coniferous forests above 2500 m, while *M. flexuosum* is often solitary and is a plant of wet, broad-leaf cloud forests below 2500 m. The rhizome of *M. flexuosum* is broader, less elongate, and more densely packed with starch, especially in the distal portions. The inflorescence of *M. flexuosum* is pendent rather than upright and is at least slightly flexuous, the tepals are usually tinted with lavender, and the stamens are generally inserted 1 mm or so above the tepal bases.

5. *Maianthemum gigas* (Woodson) LaFrankie, comb. nov.

Smilacina gigas Woodson, Ann. Missouri Bot. Gard. 27: 270. 1940. TYPE: Panama, Chiriquí, trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, 14 Jan. 1939, *P. Allen* 1446 (holotype, MO!; isotype, GH!).

Terrestrial or sometimes epiphytic herb, 0.8–2.5 m tall. Roots uniform, 10 to 15 per rhizome unit, evenly scattered, 30–60 cm by 2–4 mm. Rhizome a

Morphometric comparison of inflorescences of *Maianthemum scilloideum* and *M. flexuosum*.*

CHARACTER	<i>M. scilloideum</i>			<i>M. flexuosum</i>		
	RANGE	ME- DIAN	MEAN	RANGE	ME- DIAN	MEAN
Inflorescence length (cm)	1.6–8.3	2.9	2.9 ± 0.9	5–18	9.1	10.4 ± 1.4
Flowers per inflorescence	4 to 27	15	15.5 ± 2.5	8 to 65	30	34.8 ± 5.6
Flowers per fascicle	1 to 3	3	2.5 ± 0.2	2 to 6	3	3.2 ± 0.3
Pedicel length (mm)	3–4.5	4	4.2 ± 0.5	8–21	14.5	14.5 ± 1.4

*Results expressed as range, median, and mean with 95% confidence interval.

massive, forking sympodium, the individual units broad-claviform to sub-spherical, 3–4 cm broad, the scale leaves 8 or 9, the internodes 2–5 mm long, the lateral buds 6 or 7, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch only near rhizome apex. Leafy stem leaning or arching, 75–250 cm long, 8–15 mm broad at base, the surface smooth, glabrous; foliage leaves 10 to 16; internodes 3–5.5 cm long. Leaves with petiole 4–5 mm long; blade ovate to elliptic, 14–30(–38) by 5–9(–11) cm, the apex acuminate, the base tapered or rounded, the margin undulating, denticles distinct but very small, the veins ranked, the surfaces glabrous. Inflorescence a pyramidal panicle with 45 to 400 flowers; main axis arching upward, straight, stiff, 15–29 cm long, 2.5–4 mm broad at base, ribbed, light green-white, or red-purple, glabrous; internodes 25 to 30, most 2–15 mm long; lateral branches racemose, arranged in helix, spreading or slightly ascending, 6–15 cm long, with 1 or 2 flowers at base and others inserted at 1–4(–10) mm intervals, bract subtending each lateral raceme. Flowers trimerous; pedicel 2–5(–7) by 0.5–0.8 mm, deeply ribbed, glabrous, with bract subtending; tepals uniform, spreading, (2.5–)3–5 by 1.3–2.3 mm, white, sometimes with purple spots; stamens inserted at tepal base, the filament 2–3.5 mm long, thin, the anther oblong, 0.5–1 mm long; ovary spherical to cylindrical, 1–1.5 mm in diameter, the style 0.8–1.2 mm long, the stigma 3-lobed, 0.7–1 mm broad. Fruits spherical to weakly 3-lobed, 10–12 mm broad, green mottled with red when young, maturing to red; seeds up to 6, usually spherical, 4–6 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

The Central American species of *Maianthemum* with paniculate inflorescences are often difficult to identify from herbarium material alone, which is perhaps why previous taxonomic treatments of this group have lumped all such specimens under “*M. paniculatum*.” The flowers are relatively uniform when dried, and the species differ chiefly in the shape of the rhizome, the number of foliage leaves, and the form of the inflorescence. The rhizome and the foliage leaves are often missing from herbarium specimens, and the question of inflorescence morphology is often confounded by uncertainty as to the plant’s level of maturity. A rule of thumb helpful in determining maturity is that a plant is full size when the length of the inflorescence exceeds that of the pen-

ultimate foliage leaf. Despite this information, many immature shoots within the paniculate group cannot be adequately identified.

I have recognized four species (*Maianthemum paniculatum*, *M. gigas*, *M. paludicolum*, *M. septifolium*) and two varieties bearing paniculate inflorescences. The species can be identified by several vegetative features, and although I suspect that floral differences are also present, they are not easily observed in dry material. Potentially useful floral features include shape of the ovary, morphology of the septal nectary and pore, number of ovules, and color of immature fruit. The present treatment of the paniculate group is an improvement over the aggregation of all types within a single species, but it remains unsatisfactory in its failure to identify decisive floral differences between species. The plants of western Panama are especially diverse. Woodson and Schery (1940) determined that the very large plants of Panama were a new species (*M. gigas*) and were clearly distinct from the smaller and more widespread plants, which they took to be *M. paniculatum*. Later, Woodson and Schery (1945) reduced *M. gigas* to the synonymy of the latter species. My study of this group throughout Meso-America indicates that Woodson was originally correct in his analysis, but I was unable to determine any consistent difference in floral morphology between the two species. Further study on this point should be directed toward western Panama, where they both occur, and field study of floral morphology should be emphasized.

As mentioned, there are many singular collections that fall within the range of *Maianthemum gigas*, but I recognize only the previously described taxon *M. gigas* var. *crassipes* as distinct, and I would suggest that any new varieties in this species be based on field study rather than on herbarium specimens alone.

Key to the Varieties of *Maianthemum gigas*

- Tepals 5–7 by 3–3.5 mm, yellow or yellow-white; perianth cupuliform; pedicel 0.8–1 mm broad. 5a. var. *crassipes*.
 Tepals 2.5–5 by 1.5–2 mm, white or white infused with lavender; perianth spreading; pedicel 0.4–0.7 mm broad. 5b. var. *gigas*.

5a. ***Maianthemum gigas* var. *crassipes*** (Standley & Steyermark.) LaFrankie, comb. et stat. nov. FIGURE 10A–G, MAP 5.

Smilacina crassipes Standley & Steyermark. Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 214, 215. 1947. TYPE: Guatemala, Huehuetenango, Cerro Pueblo Viejo, rocky slope above La Libertad, 1900 m, 20 Aug. 1942, *Steyermark 51003* (holotype, F (F no. 1129142!); isotype, F!).

Terrestrial or epiphytic herb, 0.7–1.3 m tall. Roots not seen. Rhizome not seen. Leafy stem arching or pendent, 70–130 cm long, glabrous. Leaves with petiole 2–4 mm long. Inflorescence a diffusely flowered pyramidal panicle with 40 to 130 flowers; main axis straight, stiff, tapering, 10–15 cm long, 3–4 mm wide at base, deeply ribbed, green, glabrous; internodes 25 to 30, most 2–6 mm long; lateral axes with 5 to 7 flowers. Flowers with pedicel 5–8 by 0.8–1 mm, deeply ribbed, glabrous; perianth suberect or cupuliform at anthesis; tepals 7–9 by 3–3.5 mm, pale yellow; stamens with filament 3–5 mm long, thin,

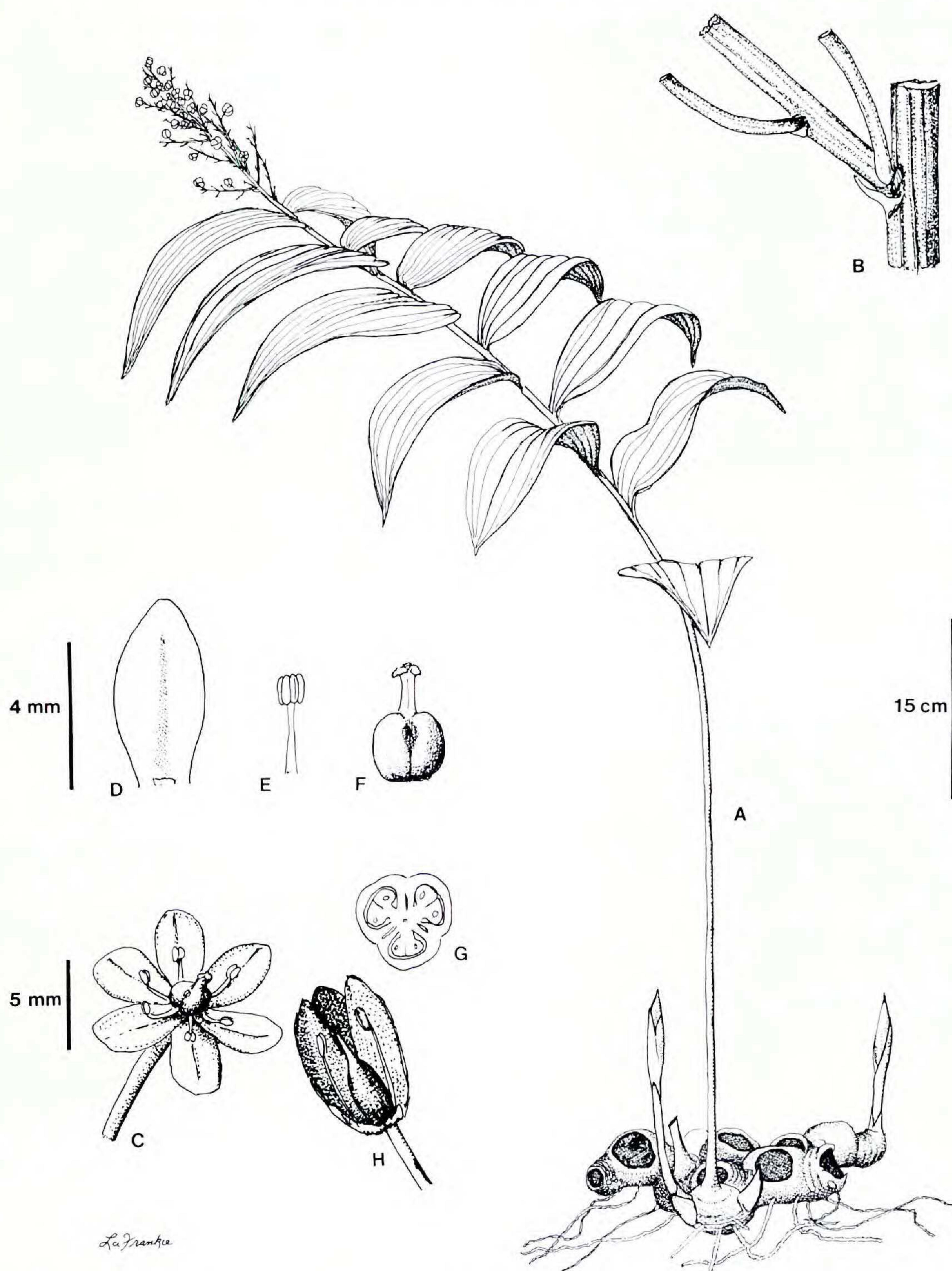
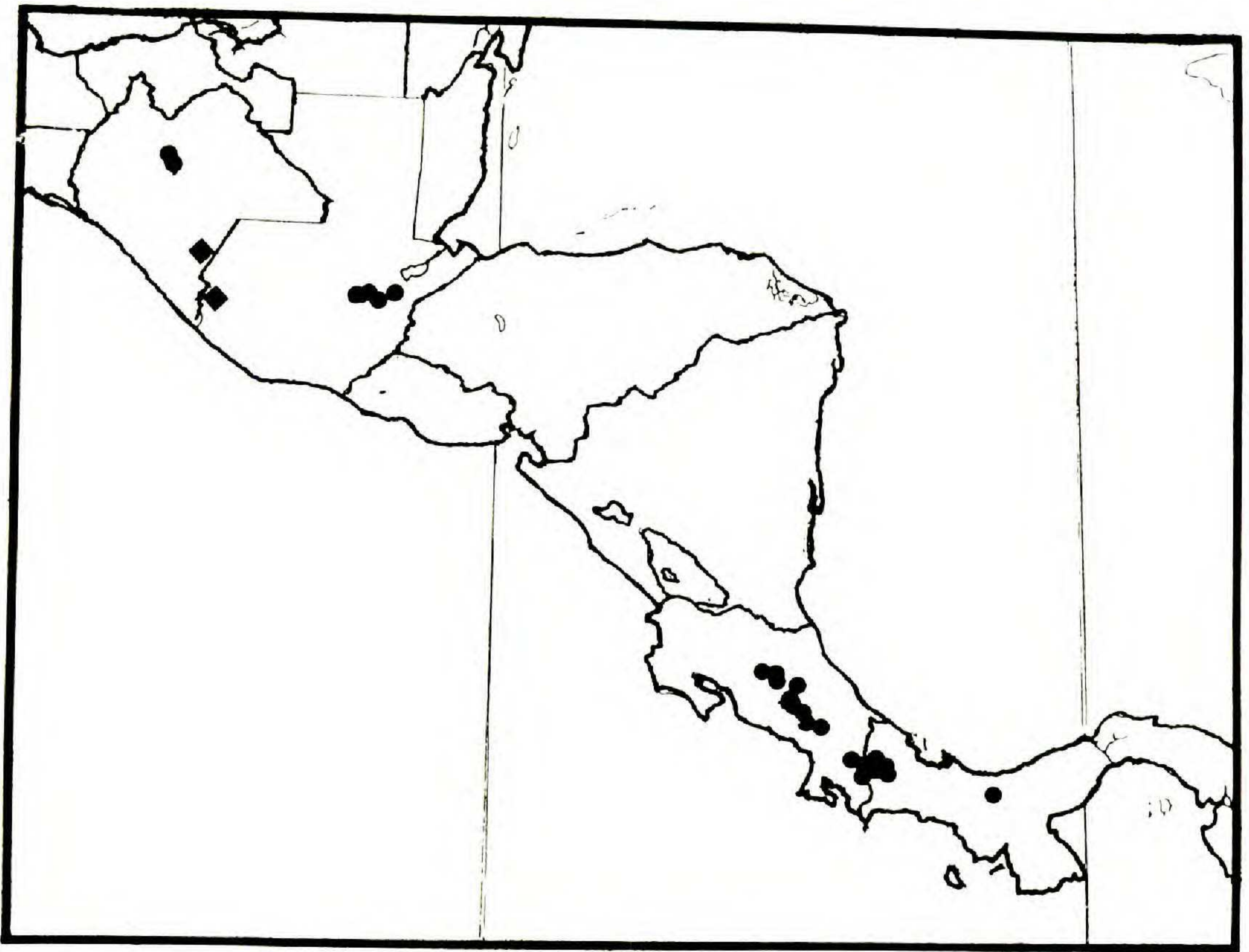


FIGURE 10. *Maianthemum gigas*. A–G, var. *gigas* (LaFrankie 83-IV-10A, GH): A, rhizome, leafy shoot, and infructescence; B, detail of lateral raceme of infructescence; C, flower; D, tepal; E, stamen; F, gynoecium; G, ovary, transverse section, showing 6 ovules, 3 cavities of septal nectaries. H, var. *crassipes* (Matuda 4702, LL), flower.

anther 1.2–1.6 mm long; ovary cylindrical, 2.5–3 by 1.5–2 mm, the style 1.5–2.4 mm long, the stigma 3-lobed, as broad as style. Fruits spherical, 8 mm in diameter, red when mature; seeds 1 to 6, oblong-cuneate, 2.5–3.5 mm long. Chromosome number not known.



MAP 5. Distribution of *Maianthemum gigas*: var. *gigas* (dots) and var. *crassipes* (diamonds).

ECOLOGY AND DISTRIBUTION. Very rare (known from three collections only); described once as an epiphyte, twice as terrestrial ("on rocks"?) at 1900 m alt. Guatemala, and Chiapas, Mexico.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mt. Malé, near Porvenir, [Arroyo?] Potrero, 3200 m, *Matuda* 4702 (LL, MO). **Guatemala.** SAN MARCOS: Finca El Porvenir, Potrero Tojo, Volcán Tajumulco, 1300–1350 m, *Steyermark* 37655 (F).

Maianthemum gigas var. *crassipes* is a very rare and little-known taxon. It is similar to other large, paniculate species of Central America, and because of its large leaves and flowers I align it with *M. gigas* (see further discussion of the paniculate species and varieties under the species heading).

5b. *Maianthemum gigas* var. *gigas*

FIGURE 10H, MAP 5.

Terrestrial or sometimes epiphytic herbs, 0.8–2.5 m tall. Leafy stem leaning or arching, 75–250 cm long, 8–15 mm broad at base, the surface smooth, glabrous. Leaves with petiole 4–5 mm long. Inflorescence a dense pyramidal panicle with 50 to 400 flowers; main axis arching upward, stiff, 15–29 cm long, 2.5–4 mm wide at base, ribbed, light green-white, or red-purple, glabrous; lateral axes with 10 to 20 flowers. Flowers with pedicel 2–5(–7) by 0.4–0.7 mm, deeply ribbed, glabrous; tepals uniform, spreading, (2.5–)3–5 by 1.3–2.3 mm, white, sometimes with purple spots; stamens inserted at tepal base, the

filament 2–3.5 mm long, thin, the anther subspherical, 0.5–1 mm broad; ovary spherical to cylindrical, 1–1.5 by 1–1.5 mm, the style 0.8–1.2 mm long, the stigma 3-lobed, 0.7–1 mm broad. Fruits spherical to weakly 3-lobed, 8–10 mm broad, green mottled with red when young, maturing to red; seeds up to 6, usually spherical, 4–6 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Widespread, with broad ecological range. Most often terrestrial along roadsides, in secondary vegetation or openings, sometimes persisting in shade; also epiphytic to height of several meters. Flowering and fruiting throughout year, but less commonly January–March.

Widely distributed throughout most of Meso-America; rare in Chiapas, scattered in Guatemala (in Sierra Madre del Sur and Sierra Las Minas), common above 2000 m alt. in Costa Rica and western Panama.

SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Pueblo Nuevo Solistahuacán, *Tillet 636-20* (US). **Guatemala.** ALTA VERAPAZ: road to Finca Sepacuité, 3850–4000 ft, *Luteyn 3538* (DUKE). **Costa Rica.** HEREDIA: between San Rafael and Río Las Vueltas, *D. Stevens 13930* (MO); Volcán Barba, *Utley 2313* (F), *Wilbur 17058* (DUKE, F). SAN JOSÉ: between Canaan and Chirripó, above Río Talari, *Burger 7414* (F), *8321* (F). CARTAGO: Volcán Irazú, *Allen 690* (F, GH), *Lems 650129* (NY), *Rodriguez 175* (UC), *Seibert 1636* (MO), *Stork C463* (UC, US); Volcán de Turrialba, *Standley 35186* (F); 10 km S of Hacienda Tapanti, *Burger 5648* (F); Parque Nacional Chirripó, *Davidse 24838* (MO); San Rafael de Oreamuno, *Echeverria 469* (F). LIMÓN: Cerro Kámuk, *Davidse 26009* (MO). **Panama.** BOCAS DEL TORO: headwaters of Río Culubre, *Davidse 25204* (MO). CHIRIQUÍ: vic. Cerro Punta, *Croat 48624* (MO), *Luteyn 3810* (DUKE), *4623* (DUKE), *4626* (DUKE), *Mori 5657* (MO), *7239* (MO), *Sytsma 2081* (MO), *Wilbur 13204* (F, GH, LL, MICH, MO, NY), *24218* (DUKE), *24253* (DUKE); Palo Alto, E of Boquete, *Stern 1062* (GH, MO, UC, US); above Boquete, *Croat 15754* (DUKE), *Lewis 559* (MO); Cerro Pato de Macho, 5 mi NE of Boquete, *Antonio 2676* (MO), *D'Arcy 12635* (MO); Cerro Colorado, *Antonio 1408* (MO), *Folsom 1772* (MO); vic. Bajo Mona and Quebrada Chiriquí, *Woodson 512* (GH, MO, NY); Bajo Chorro, *Davidson 53* (F, GH, MO, US); Cerro Respinga, *Gentry 5913* (MO); Cerro Horqueta, *Hagar 2017* (MO). VERAGUAS: N of Santa Fe, Cerro Arizona, *Hammel 4712* (MO); vic. Santa Fe, trail to Cerro Tute, *Antonio 1979* (MO).

6. *Maianthemum macrophyllum* (M. Martens & Galeotti) LaFrankie, Taxon **35**: 588. 1986. FIGURE 11, MAP 4.

Smilacina macrophylla M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **9**: 387. 1842. TYPE: Mexico, Veracruz, on oaks near Jalapa and Totutla, 3000–4000 ft, 1840, *Galeotti 5473* (lectotype, here chosen, BR (BR no. 3394/84-2!); isoelectotype, BR (BR no. 3394/84-3!)).

Epiphytic herb, 0.75–1.25 m tall. Roots uniform, fewer than 15 per rhizome unit, evenly scattered, length not known, 1–2 mm broad. Rhizome a forking sympodium, the individual units subspherical, 4–7 cm broad, the number of scale leaves not known, the internodes uniform, 2–5 mm long, the lateral buds at most internodes, axillary; epidermis replaced by periderm; carbohydrate reserves not known. Leafy stem slightly arching, 75–120 cm long, 5–9 mm broad at base, glabrous, polished; foliage leaves 13 to 18; internodes 2.5–4 cm long, shorter apically. Leaves with petiole 5–9 mm long; blade ovate to lanceolate, upper ones 14–21 by 4.5–8 cm, lower ones 10–16 by 5–8 cm, the apex

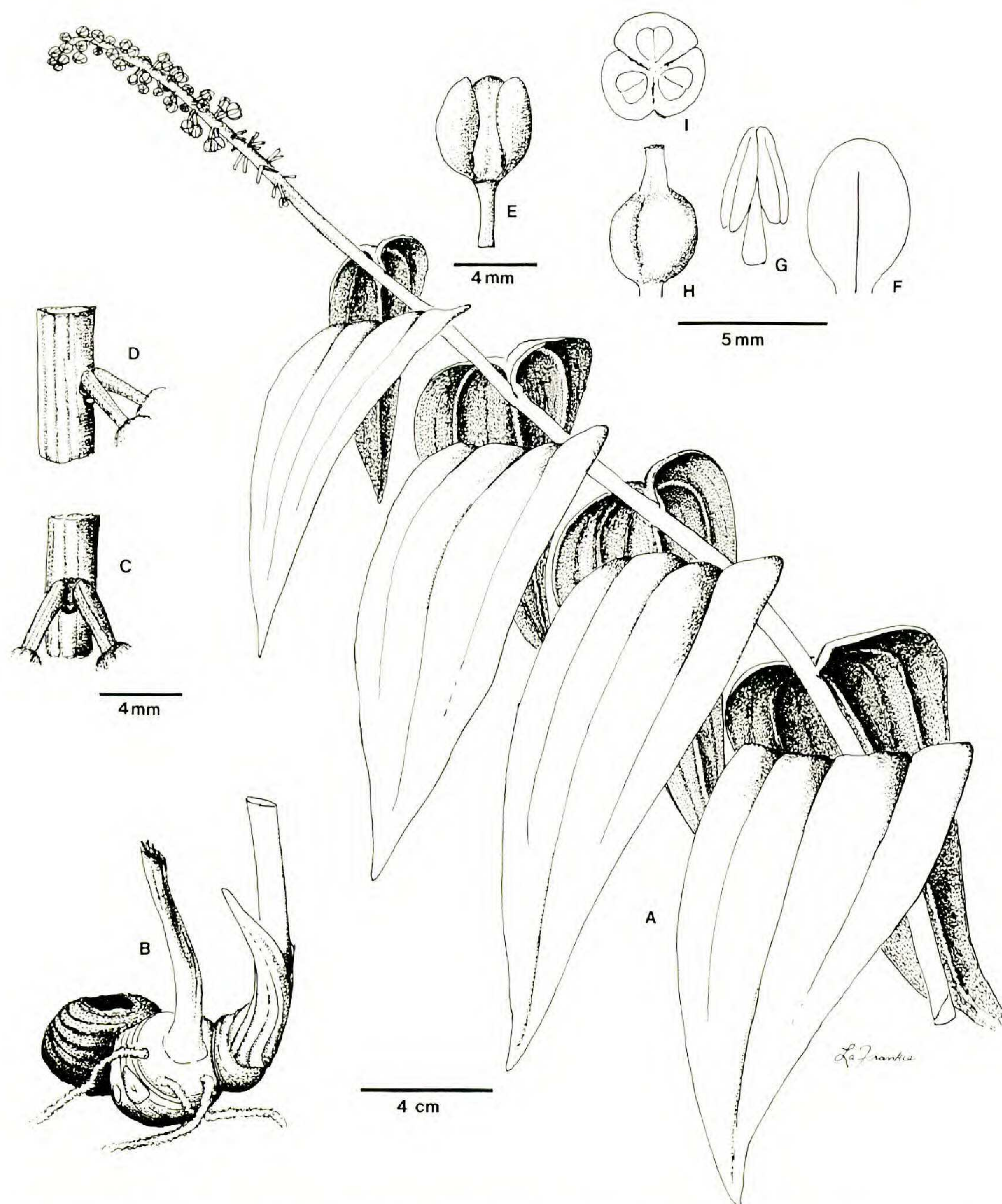


FIGURE 11. *Maianthemum macrophyllum* (LaFrankie 84-V-11A, GH): A, upper portion of leafy shoot and inflorescence; B, rhizome; C, D, lateral fascicles; E, flower at anthesis; F, tepal; G, stamen; H, gynoecium; I, ovary, transverse section, showing 3 locules, 6 ovules (6 other ovules beneath).

acuminate, the base rounded, the margins flat, with denticles only near apex, the veins ranked, the surfaces glabrous, polished. Inflorescence a dense complex raceme with 60 to 120 flowers, columnar; main axis arched upward, straight, stiff, of uniform width, 10–20 cm by 2–4 mm, green, smooth, polished; internodes 25 to 50, 5–10 mm long; lateral fascicles arranged in helix on main axis, each with 2 to 4 flowers and with bract subtending. Flowers trimerous; pedicel reflexed, (2–)4–6(–9) by 0.5–1 mm, smooth, glabrous, with bract subtending;

perianth cupuliform, the tepals uniform, 4.5–5.5 by 2–3 mm, yellow-green to green-white, stamens inserted at tepal base, 2–3 mm long, the filament 1.5–2.5 mm long, thin, the anther 1–1.5 mm long; ovary 2–3 by 1.5–2.5 mm, the style 1–1.5 mm long, the stigma 3-lobed, narrow. Fruits spherical, 8–9 mm in diameter, green when young, maturing to red; seeds 6 to 12, cuneate, 2.5 mm broad. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Rare; usually on canopy branches of oaks or *Liquidambar*, in primary cloud forests; 1350–2000 m alt. Flowering April–June, with flowers opening acropetally over 3–4 weeks; fruiting through October.

Endemic to Veracruz, Mexico.

SPECIMENS EXAMINED. **Mexico.** VERACRUZ: Coacoatzintla, *Castillo 117* (F, XAL); Jico, *Chazaro 1055* (MEXU, XAL); Huitamalco, *Liebman 14635* (F, MICH); Río Jamapa, *Lot 1181* (GH); Acultzingo, *Matuda 1151* (MICH, US); Santa Rita, *Ortega 2034* (XAL); Teocelo, near Jalapa, *Pringle 7854* (GH, US); Orizaba, *Reko 72* (GH); vic. Orizaba, *Weaver 1760* (DUKE, F, MICH); vic. Atzapan, Cerro Hucapan, *Rosas 352* (GH, K, MEXU); between Atzacán and Rincón Grande, *Rosas 381* (GH, MEXU); near El Puerto, *Sharp 44709* (MEXU); between Atzacán and Dos Ríos, *Sohmer 9520* (MEXU); Magdalena, *Valdivia 2175* (XAL).

Maianthemum macrophyllum is most easily distinguished by its dense columnar inflorescences and its cupuliform flowers. As an epiphyte of primary vegetation, it may be in some danger of extinction, although it is currently cultivated in the Botanical Garden of INIREB in Jalapa, Mexico. Despite the fact that most of the locations cited above have been deforested, there are still many unexplored areas along the Veracruz-Oaxaca border with forests that are the preferred habitat for this taxon.

The tepals of *Maianthemum macrophyllum* are never reflexed, nor are they fused as in *M. henryi* of China. Hara (1975) has shown the various degrees of fusion found among the Asian species, but no New World species shows any tendency toward a fused corolla.

7. *Maianthemum monteverdense* LaFrankie, sp. nov. FIGURE 12, MAP 2.

A speciebus aliis *Maianthemii* in racemo complexo pendulo, 12–20 cm longo, axe principale 2–4 mm lato, pedicello 1–2.5 cm longo, 1–1.5 mm lato, fructu 1–1.5 cm lato, semine 12, differt.

Epiphytic herb, ca. 0.8 m tall. Roots uniform, 8 to 10 per rhizome unit, evenly scattered, 30–60 cm by 1–2 mm. Rhizome a dense forking sympodium, the individual units subspherical, 4–6 cm broad, the scale leaves 8 to 10, the internodes 2–3 mm long, the lateral buds ca. 8, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch near rhizome apex only. Leafy stem arching, 60–85 cm long, 8–12 mm broad at base, surface smooth, polished; foliage leaves 12 to 16; internodes 4–8 cm long, shorter apically. Leaves clasping or with petiole 1–2 mm long; blade ovate to lanceolate, 13–15 by 9–10 cm, the apex acute to tapered-acuminate, the base rounded, the margin flat, with denticles inconspicuous and appressed, the veins ranked, the surface glabrous, polished. Inflorescence a complex raceme (lower fascicles

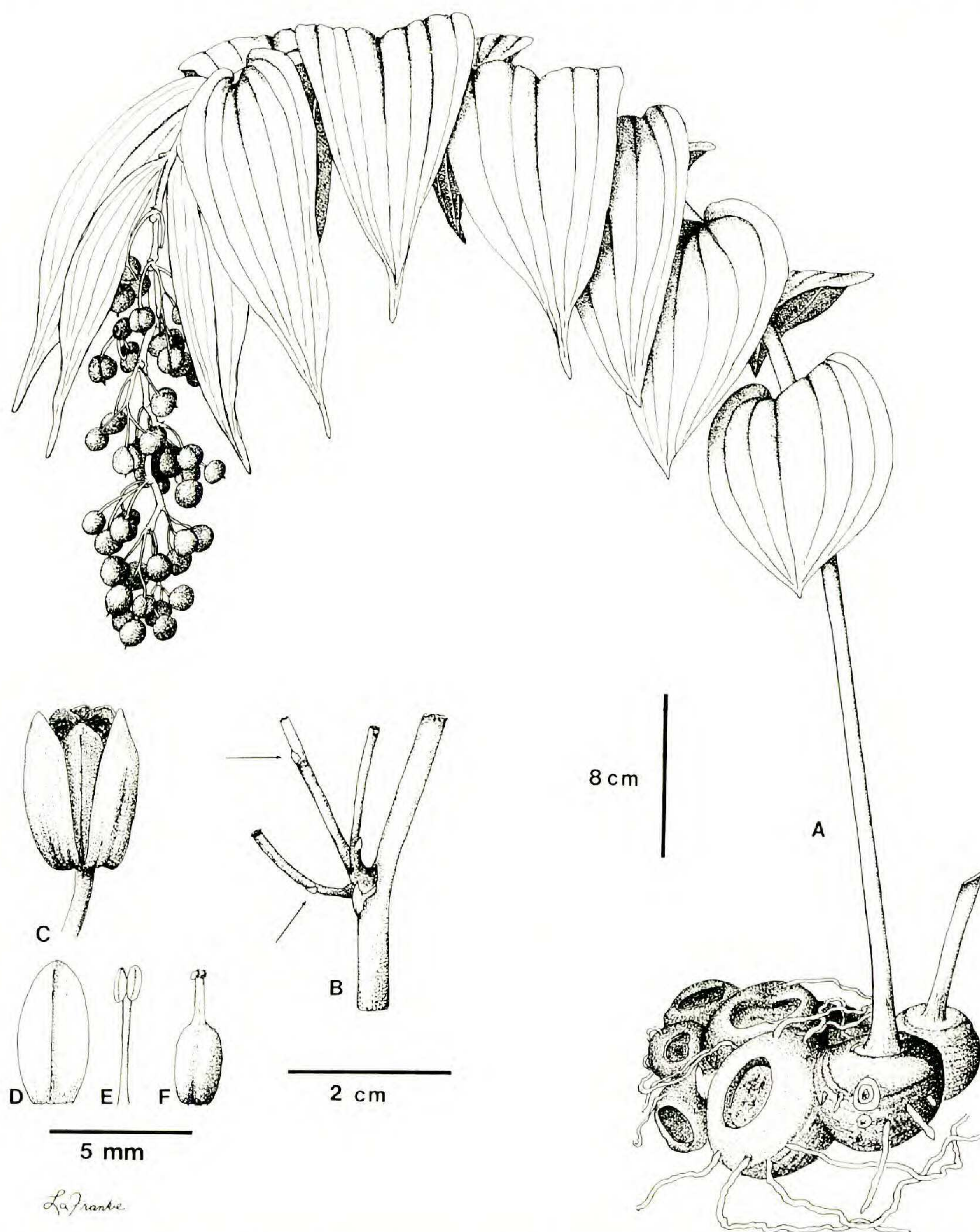


FIGURE 12. *Maianthemum monteverdense*: A, rhizome, leafy shoot, and infructescence; B, detail of lateral branch of infructescence; C, flower; D, tepal; E, stamen; F, gynoecium. (A, B based on *LaFrankie 83-IV-14B*, GH; C-F on *Luteyn 4506*, DUKE.)

sometimes congested racemes < 5 cm long) with 40 to 60 flowers; main axis pendent, slightly flexuous, 15–20 cm long, 3–5 mm broad at base, smooth, light green, polished; internodes 1–2 cm long; lateral branches in helix, spreading, with 4 to 6 flowers clustered on short axis. Flowers trimerous; pedicel 10–25 by 0.8–1.2 mm, smooth, glabrous, with bract inserted between base and midpoint; perianth cupuliform, the tepals uniform, 5–5.5 by 2 mm, yellow-green; stamens inserted at tepal base, 2–3 mm long, the filament 1.5–2 mm

long, thin, the anther oblong, ca. 1 mm long; ovary cylindrical, ca. 2 by 1 mm, the style 1.5 mm long, the stigma 3-lobed, ca. 1.5 mm broad. Fruits 3-lobed, 10–12 mm broad, green when young, maturing to red; seeds 2 to 12, slightly flattened, 1.5–2 mm wide. Chromosome number not known.

TYPE. Costa Rica, Alajuela, Monteverde Forest Preserve, Pantano Chomogo, 1600–1620 m, *Dwyer 1408* (holotype, F!).

ECOLOGY AND DISTRIBUTION. Cloud forests, persisting in blowdowns as long as canopy remains open; 1600–1700 m alt. Flowering December–February; fruits retained through August.

Relatively restricted distribution; most collections from Cordillera de Tilarán in northern Costa Rica.

SPECIMENS EXAMINED. **Nicaragua.** JINOTEGA: [northern spur of Cordillera Isabella,] Cerro San Pedro, Monte Kilambe, *P. Moreno 7516* (MO). **Costa Rica.** ALAJUELA: Reserva Forestal, San Ramón, *Carvajal 135* (MO), *346* (MO); 15 km NW of San Ramón, Cerro Azahar, *Liesner 15620* (MO); 12 km NW of San Ramón, *Judziewicz 14906* (MO); Monteverde Forest Preserve, NE section, 1600–1700 m, *LaFrankie 83-IV-14B* (GH), *Utley 2379* (F); road out of Sucre toward Pozo Verde, toward Cerro Porvenir, *Luteyn 4506* (DUKE). HEREDIA: S slope of Volcán Barba, *Hatheway 1372* (US).

The form of the lateral racemes (each consisting of a few flowers borne on long pedicels that are drawn together, with the subtending bract usually adnate and repositioned at the midpoint of the pedicel) associates this species with the more northern *Maianthemum amoenum*. Also, both species are epiphytes. However, *M. monteverdense* differs from *M. amoenum* in having a long, pendent inflorescence rather than a short, erect one and in lacking the red coloring in the central axis of the inflorescence. It is also larger in most vegetative dimensions.

8. ***Maianthemum paludicolum*** LaFrankie, Amer. J. Bot. **73**: 1258. 1986. TYPE: Costa Rica, Cartago, 17 km S of Empalme along Pan-American Highway, 2500 m, 22 Sept. 1985, *LaFrankie & Beach 85-23* (holotype, GH!).

FIGURE 13, MAP 4.

Terrestrial herb, 1 m or more tall. Roots uniform, 2 to 4 per rhizome unit, aggregated at branch junctions, up to 60 cm by 1–2 mm. Rhizome a linear or forking sympodium, mostly exposed and upright, the individual units long-cylindrical, 10–45 cm by 7–20 mm, the scale leaves 7 to 9, the first and last internodes 2–5 mm long, middle ones 3–25 cm long, the lateral buds 2, at base of leafy shoot, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; distribution of starch not known. Leafy stem upright, slightly flexuous, 35–65 cm long, 3–4 mm broad at base, glabrous; foliage leaves 9 to 12 (to 14); internodes 1.5–3 cm long. Leaves with petiole 1–2 mm long; blade ovate to lanceolate, upper ones 10–15 by 2–4.5 cm, lower ones 5–9 by 3–5 cm, the apex acuminate, the base rounded, the margin flat, entire, the veins of uniform strength, the surfaces glabrous. Inflorescence a pyramidal panicle with 40 to 80 (to 120) flowers; main axis upright, stiff, straight, tapering, 6–20 cm long, 1.5–2 mm wide at base, slightly ribbed, red-violet, glabrous; internodes

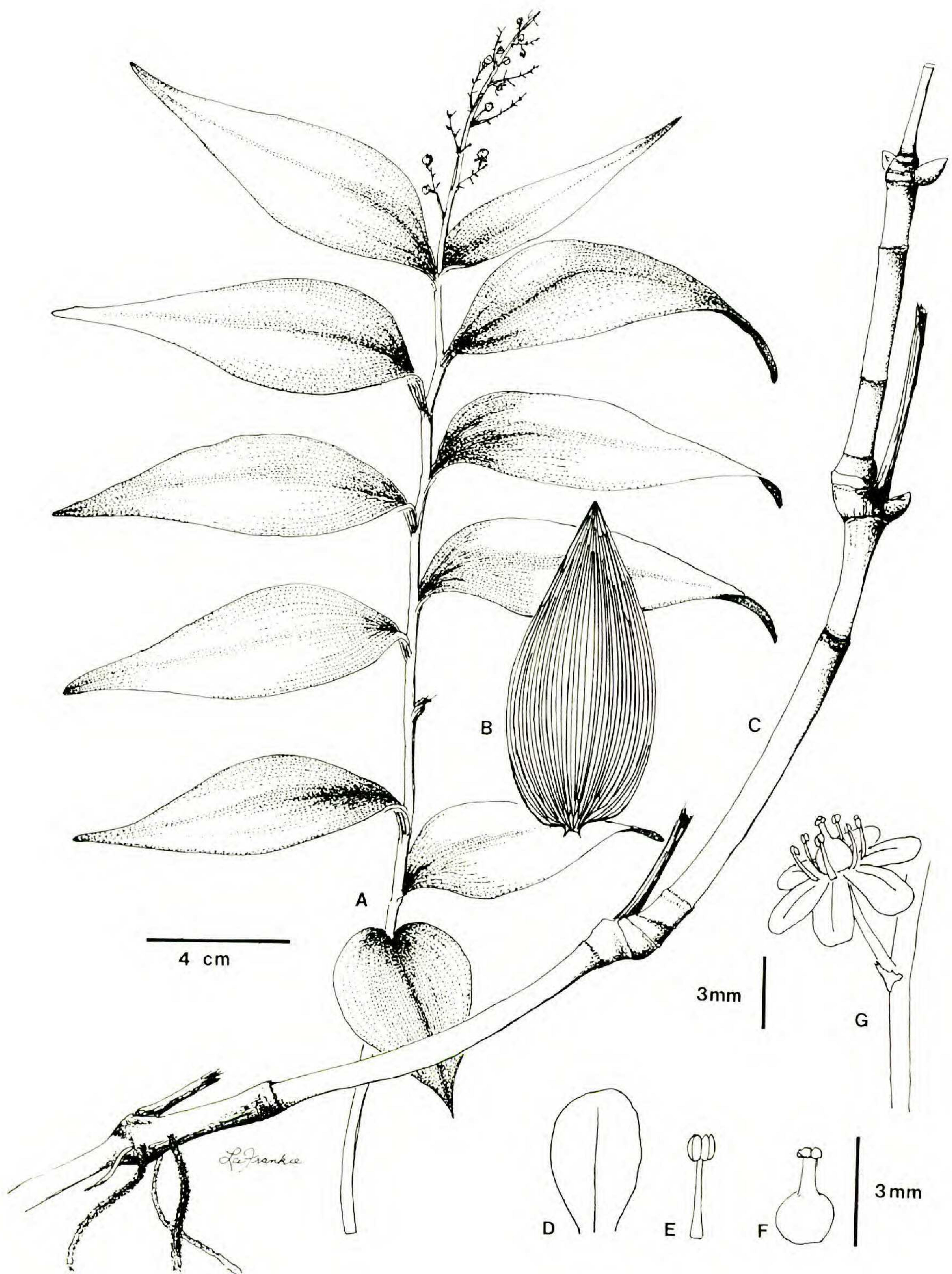


FIGURE 13. *Maianthemum paludicolum* (Jiménez 23, US): A, leafy shoot (note spreading leaves of uniform size); B, leaf, showing veins of uniform strength; C, sympodial rhizome, showing bases of old leafy stems, long scale-leaf internodes, renewal buds at base of leafy stem (renewal shoot and leafy shoot growing in same direction); D, tepal; E, stamen; F, gynoecium; G, flower on lateral raceme.

5 to 15, 3–10 mm long; lateral axes racemose, arranged in helix, spreading or slightly ascending, 3–8 cm long, 1 or 2 flowers at base and others at irregular intervals of 1.5–6 mm, bract subtending each lateral raceme. Flowers trimerous; pedicel 2–5 by ca. 0.5 mm, ribbed, glabrous, with bract subtending; tepals uniform, spreading, 3–4 by 1.5–2.5 mm, white; stamens inserted at tepal base, the filament 1–2 mm long, narrow, the anther 0.5–0.8 mm long; ovary spherical, 1–1.4 mm in diameter, the style ca. 1 mm long, the stigma 3-lobed, ca. 0.8 mm broad. Fruits spherical, 5–7 mm in diameter, red at maturity; seeds 1 to 3, spherical, ca. 4 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Rare; alpine bogs and wet ground of central Costa Rica; 2500–2800 m alt. Flowering April–November; fruits evident throughout year.

Most frequently collected along Pan-American Highway (including powerline right of way), 10–25 km south of Empalme, but rather common throughout this open boggy site.

SPECIMENS EXAMINED. **Costa Rica.** SAN JOSÉ–CARTAGO border: 15.8 km SE of Empalme, [along Pan-Am. Highway,] *Wilbur 19907* (DUKE); 16 km SE of Empalme, *Wilbur 17546* (DUKE); 17 km SE of Empalme, *Utley 837* (F, MO); 17.6 km SE of Empalme, *Wilbur 22564* (DUKE); 18–20 km SE of Empalme, bog, *Cruz 14* (F, GH); 20 km SE of Empalme, *Burger 9553* (F), *Lellinger 1140* (F, MO, US), *Wilbur 23770* (DUKE); 9.6 mi SE of Empalme, *Wilbur 16738* (DUKE); 22 km SE of Empalme, *Burger 7985* (F, MO, NY); Ojo de Agua, *Dayton 3030* (F), *Stork 3025* (F); Río Humo, *Pochero 76* (F); Pan-Am. Highway, 8 km E of road to La Cima, *D. Stevens 13385* (F); Cerro del Muerte, sphagnum bog, *Barbour 1023* (F), *Carlson 3491* (F, GH, LL), *Carpenter 561* (US, WIS); Talamanca Range, Pacific slope, *Taylor 11807* (MO); Tres de Junio[?], Pan-Am. Highway, 2400 m, *Todzia 1323* (CR, LL).

Maianthemum paludicolum cannot be confused with the other paniculate species of Costa Rica if close attention is paid to the distinctive venation of the leaves and to their overall dimensions, as well as to the rhizome and the growth habit. The original description of this species includes an analysis of its unusual rhizome.

9. ***Maianthemum paniculatum*** (M. Martens & Galeotti) LaFrankie, Taxon **35**: 588. 1986. FIGURE 14, MAP 6.

Smilacina paniculata M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles **9**: 388. 1842; *Vagnera paniculata* (Martens & Galeotti) Standley, J. Wash. Acad. Sci. **15**: 457. 1925. TYPE: Mexico, Oaxaca, Chinantla, epiphytic on oaks, 2000–4000 ft, *Galeotti 5472* (holotype, BR (BR no. 3394/84-4!)).

Tovaria thyrsoides Baker, J. Linn. Soc., Bot. **14**: 568. 1875; *Smilacina thyrsoides* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3**: 368. 1884. TYPE: Mexico, [Oaxaca?,] Sierra San Pedro Nolasco [Cerro de Nolasco], Talea, 1843–1844, *Jurgensen 959* (lectotype, here chosen, κ!).

Tovaria nervulosa Baker, J. Linn. Soc., Bot. **14**: 569. 1875; *Smilacina nervulosa* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3**: 368. 1884. TYPE: Mexico, Veracruz, Jalapa, *Torrey 1040* (holotype, κ!).

Tovaria laxiflora Baker, J. Linn. Soc., Bot. **14**: 569, 570. 1875; *Smilacina laxiflora* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3**: 368. 1884. TYPE: Guatemala, Chilascó, 1861, *Salvin & Goodman s.n.* (holotype, κ!).

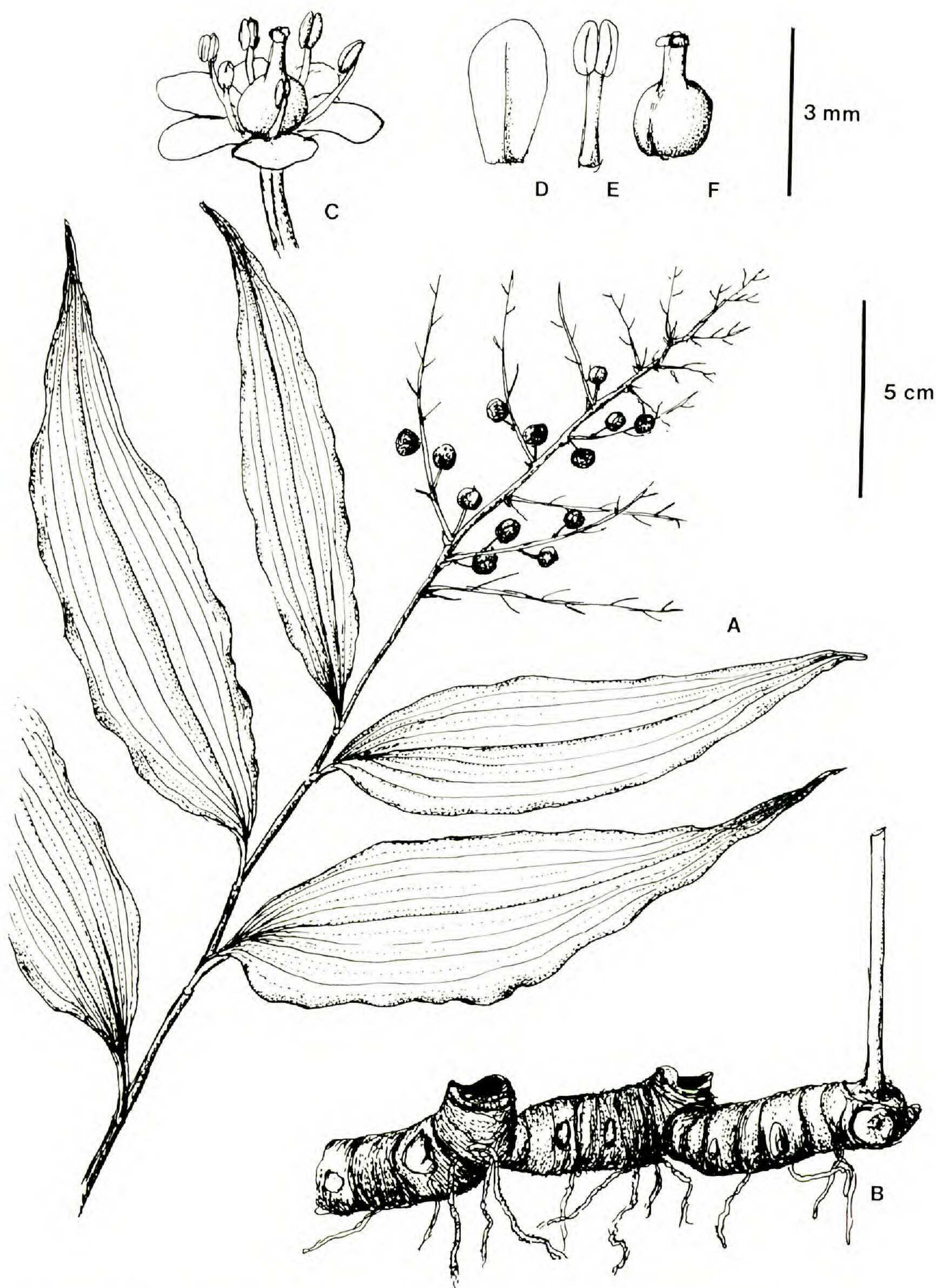
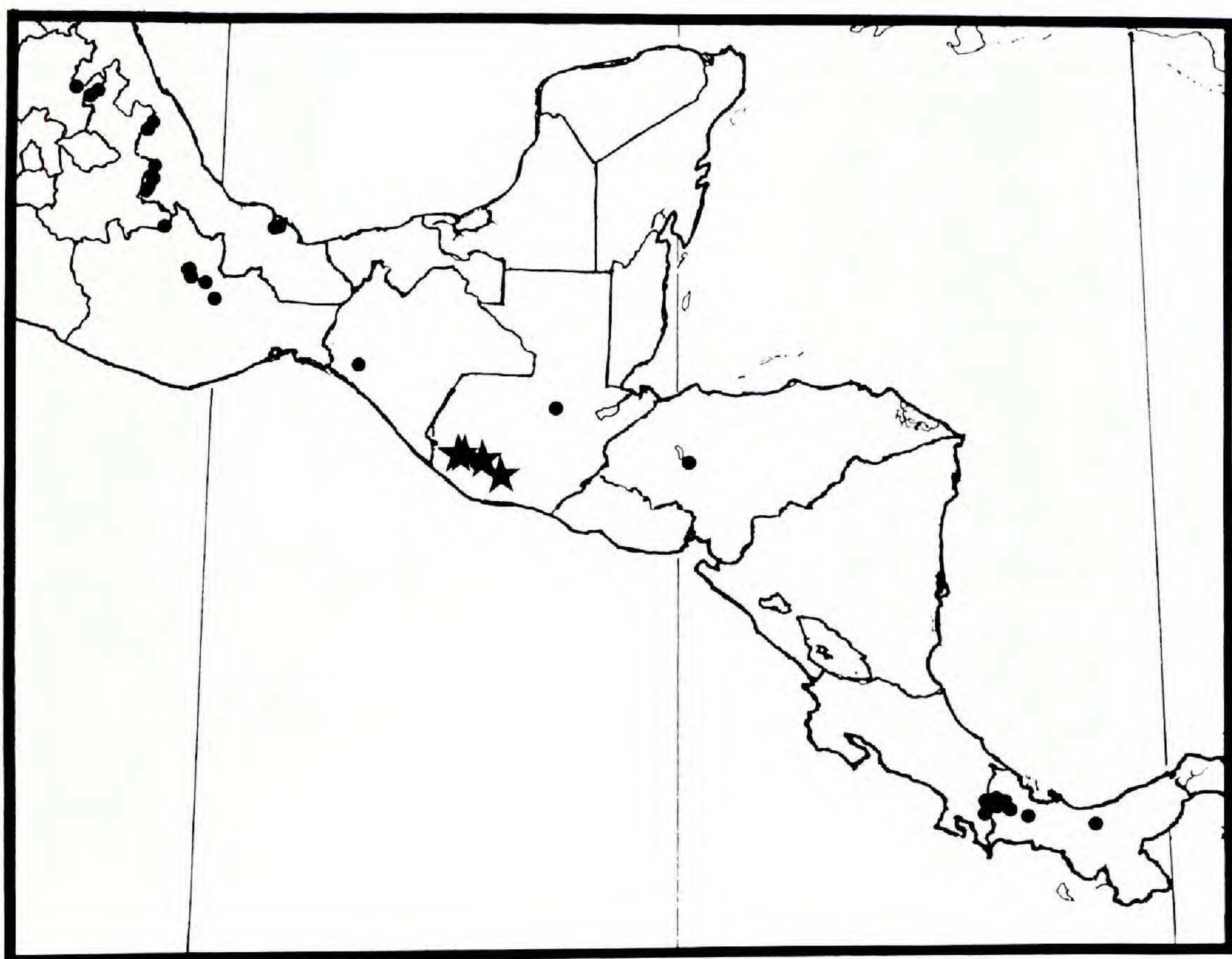


FIGURE 14. *Maianthemum paniculatum* (LaFrankie 83-IV-20, GH): A, upper portion of leafy shoot and infructescence (note widely spaced pedicels on lateral branch axes); B, rhizome; C, flower; D, tepal; E, stamen; F, gynoecium.



MAP 6. Distribution of *Maianthemum paniculatum* (dots) and *M. salvinii* (stars).

Terrestrial forest herb, 0.7–1.5 m tall. Roots uniform, 8 to 20 per rhizome unit, evenly scattered, 30–50 cm by 1–2 mm. Rhizome a forking sympodium, the individual units short-cylindrical to narrow-claviform, 2–3.5 by 2–4 cm, the scale leaves 6 or 7, the internodes 2–12 mm long, shorter apically, the lateral buds 6, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch deposited in distal portions but not dense. Leafy stem arching, leaning, or upright, 75–150 cm long, 6–8 mm broad at base, the surface smooth, glabrous; foliage leaves 10 to 15; internodes 4–6.5 cm long. Leaves with petiole 4–6 mm long; blade ovate-elliptic, 10–14 by 4–6 cm, the apex acuminate, the base tapered, the margin undulate, entire or denticulate, the veins ranked, the surface glabrous. Inflorescence a pyramidal panicle with 70 to 200 flowers; main axis arching upward, tapered, 15 cm long, 2–3 mm wide at base, weakly ribbed, smooth or with denticles, green or maroon; internodes 10 to 15, 8–20 cm long; lateral axes racemose, arranged in helix, spreading or ascending, 5–8 cm long, with 1 flower at base and others inserted at intervals of (7–)10–20 mm, with bract subtending each raceme. Flowers trimerous; pedicel 1–2 by ca. 0.4 mm, weakly ribbed, smooth or with denticles, with bract subtending; tepals uniform or weakly dimorphic, spreading, 2–3.2 mm long, white; stamens inserted at tepal base, the filaments thin, 1.4–2.2 mm long, the anthers 0.6–1 mm long; ovary spherical, 0.8–1.2 mm broad, style 0.6–1.4 mm long, stigma distinctly 3-lobed. Fruits spherical or weakly 3-lobed, 8–12 mm

broad, green, mottled with red when young, maturing to red; seeds 1 to 6, usually spherical, 5.5–6 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Common and widespread by roadsides and in light-gaps in forest, sometimes persisting in shade. Widely distributed throughout entire range of genus in Meso-America, although absent in northern and central Costa Rica. Flowering and fruiting throughout year but less common December–March.

SPECIMENS EXAMINED. **Mexico.** HIDALGO: Tenango de Doria, 1800 m, *Gimate* 966 (MEXU, MICH, MO, XAL). PUEBLA: below Honey Station, *Pringle* 8836 (CAS, F, GH, LL, MICH, NY, UC, US); between Teziutlán and Tlapacoyán, *Suacedo* 70 (DS, MICH, MS, WIS); N of Tlaltlaqui, *Boege* 1709 (MEXU). VERACRUZ: Atzalan, Tetejicapa, *Ventura* 964 (DS, F, MEXU, MICH, MS); Altotonga, *Ventura* 75 (DS, F, MICH, MO); Río Jamapa and road from Coscomatepec, *LaFrankie* 83-20 (GH), *Lot* 1170 (MEXU); 18.5 km NW of Coscomatepec, *Nee* 19729 (F, XAL); 16 km NE of Huayacocotla, *Hernandez* 1476 (F, MEXU), *Juarez* 41 (XAL); vic. Soteapan and Volcán Santa Marta, *Beaman* 5401 (MEXU, MO, XAL), 6218 (XAL), *Ortega* 1056 (XAL), 1077 (XAL), 1088 (XAL), *Sousa* 3609 (MEXU), *Vasquez* 61 (XAL); Cerro de Villa Rica, *Castillo* 1868 (XAL); Acatlán, *Ventura* 9390 (MEXU). OAXACA: Rte. 175, 28 km S of Valle Nacional, 2000 m, *King* 2115 (MICH), *LaFrankie* 84-28 (GH); Yelagaga, Yetzuconi, *Hallberg* s.n. (MEXU). CHIAPAS: E base Cerro Tres Picos, 1500–1800 m, *Breedlove* 24971 (DS, MO). **Guatemala.** BAJA VERAPAZ: on road from Cobán to Guatemala City, 3 km N of La Unión, *D. E. Stone* 3523 (DUKE). **Honduras.** COMAYAGUA: near summit of El Achiote, above Siquatepeque, *Yuncker* 6257 (F, GH, MICH, MO). **Costa Rica.** LIMÓN: Atlantic slope of Talamanca, near Panamanian border, *Davidse* 28683 (MO); vic. Puntarenas border, Cerro Nai, *Davidse* 26117 (MO); between Cerro Nai and Cerro Dudu, *Davidse* 26100 (MO). PUNTARENAS: upper Río Barú, 2010 m, *L. D. Gómez* 21469 (MO); headwaters of Río Bellavista, *L. D. Gómez* 22641 (MO). **Panama.** BOCAS DEL TORO: headwaters of Río Culubre, border with Panama, *Davidse* 25179 (MO); Valle del Silencio, *Antonio* 1624 (MO). CHIRIQUÍ: vic. Volcán Chiriquí, *Davidson* 990 (F, GH, MO, US), *Mori* 5751 (MO, NY), *Woodson* 1034 (MICH, MO, NY, US); Casita Alto, top of Cerro Copete, *Woodson* 339 (CAS, GH, MO, NY, US), 341 (MO), 342 (GH, MO, NY, US); slopes of Los Cumbres near town of Cerro Punta, *Croat* 13733 (MO); ridge N of Quebrada Iglesia, near town of Cerro Punta, *Croat* 16071 (MO, NY); Cerro Respinga, *D'Arcy* 10090 (MO), *Webster* 16541 (MO); vic. New Switzerland, *Allen* 1392 (GH, MO); N of San Felix, along continental divide, *Mori* 5794 (MO, NY); vic. Monte Lirio, Río Chiriquí Viejo, *Seibert* 184 (GH, MO, NY); 10 mi above Boquete on road to Volcán Barú, *Croat* 34837 (MO); E slope Cerro Pando, *Knapp* 1639 (MO); Fortuna Dam, continental divide, *D'Arcy* 15950 (MO); Cerro Hornito, *Mori* 7469 (MO). VERAGUAS: Cerro Tute, *Hamilton* 3988 (MO), 4002 (MO).

The type of *Maianthemum paniculatum* is undoubtedly a mixed collection. There are two sheets in BR labeled *Galeotti* 5472, but since only one corresponds with the protologue and with the many other specimens annotated *Smilacina paniculata* by Martens, I have chosen this (BR no. 3394/84-4) as the lectotype. The second sheet (BR no. 3394/84-5) is a small plant, evidently not fully mature, with six subsessile leaves (blade oblong-ovate, apex acute). The specimen was originally annotated by Martens “*S. interius* M. Martens & Galeotti” (nomen ined.), but this name was crossed out and *S. paniculata* written below by Martens. The confusion may have occurred because the collection numbers assigned by Galeotti do not correspond to the order in which the plants were collected, but to their arrangement in the descriptive treatment; that is, all of

Galeotti's collections described under *Smilacina* have collection numbers in sequence, even though they were collected in widely separated localities.

The Mexican specimens identified by Baker as separate species are not distinct from the variable *Maianthemum paniculatum*. Two species, *Tovaria laxiflora* and *T. nervulosa*, were based on single specimens of immature plants, while the five specimens listed under *T. thyrsoides* are easily placed in *M. paniculatum*, the type of which Baker did not see. The lectotype was chosen from the syntypes by virtue of its correspondence to the description.

The distinction between *Maianthemum paniculatum* and *M. gigas* is discussed in association with the description of the latter species, but a further note on the variation of *M. paniculatum* in Panama is warranted by the great differences in size and habit the plant exhibits there. Two forms are remarkable in their singularity yet are insufficiently known to be described at this time. The first is a very small epiphyte with a narrow, very elongate rhizome, found in the vicinity of Cerro Hornito and represented by *Folsom* 7225 (MO), *Hammel* 2340 (MO), and *Knapp* 4215 (MO). The second is another epiphyte, this with a much-extended and sparsely flowered inflorescence bearing large cupuliform flowers and very large fruits, found in the vicinity of the Fortuna Dam site and represented by *Van der Werff* 6620 (MO). This plant is also notable because it was recently collected in this area below 1000 m alt. The paniculate species of *Maianthemum* in western Panama require further study, especially with regard to fine details of the flower.

10. ***Maianthemum racemosum*** (L.) Link, Enum. Hort. Berol. Alt. 1: 343. 1821.

Terrestrial forest herb, 0.75–1.25 m tall. Roots uniform, 6 to 10 (to 30) per rhizome unit, scattered but mostly near base of leafy shoot, 30–60 cm by 0.5–2 mm. Rhizome a linear, horizontal sympodium, the individual units cylindrical, 30–40 by 8–14 mm, the scale leaves 8 to 10, the internodes 5–8 mm long, shorter apically, the lateral buds 2 or 3, 2 axillary, most proximal bud displaced to lower side of rhizome, 1 (rarely 2) developing as leafy shoot; epidermis persistent; starch in immature renewal shoot only. Leafy stem simple, stiff, upright, 75–125 cm long, 7–9 mm broad at base, ribbed, pubescent or glabrous; foliage leaves 7 to 12; internodes 2.5–5 cm long, shorter apically. Leaves clasping and sessile, or with petiole 2–6 mm long; blade elliptic to ovate, 9–17 by 4.5–7.5 cm (upper ones), ovate, 9–14 by 5–8 cm (lower ones), the apex acute or caudate, the base rounded or tapered, the margin undulate, denticles distinct, the veins ranked, the surfaces pubescent or rarely glabrous. Inflorescence a pyramidal panicle with 70 to 250 flowers; main axis upright or arched upward, stiff, straight, 7–20 cm long, 2–3 mm wide at base, ribbed, green or yellow-green, pubescent or glabrous; internodes 7 to 30, 3–15 mm long; lateral axes racemose, arranged in helix, spreading or slightly ascending, 1–6 cm long, with 2 flowers at base and others at 1–4 mm intervals. Flowers trimerous; pedicel 0.5–1 mm by ca. 0.5 mm, ribbed, pubescent or glabrous, with bract subtending; perianth inconspicuous, the tepals spreading or reflexed, ca. 1 by ca. 0.5 mm, white; stamens inserted at tepal base, the filament petaloid to subpetaloid, 0.5–1 mm long, the anther 0.5–1 mm long; ovary ca. 1 by ca. 1 mm, style 0.1–0.3

mm long, stigma obscure. Fruits spherical to 3-lobed, 4–6 mm broad, green mottled with copper spots when young, maturing to translucent red; seeds up to 4, spherical, 2.5–4 mm in diameter. Chromosome number $2n = 36, 72, 144$ (Kawano & Iltis, 1966).

Key to the Subspecies of *Maianthemum racemosum*

- Stem upright; leaves sessile, clasping, the base rounded, the apex of third leaf below inflorescence acute, with tip < 2 mm. 10a. subsp. *amplexicaule*.
 Stem arching; leaves with the petiole 2–6 mm, the base tapered, the apex of third leaf below inflorescence caudate, with tip 12–25 mm. 10b. subsp. *racemosum*.

10a. *Maianthemum racemosum* subsp. *amplexicaule* (Nutt.) LaFrankie, stat. nov. FIGURE 15H, I; MAP 7.

Smilacina amplexicaulis Nutt. J. Acad. Nat. Sci. Philadelphia **7**: 58. 1834; *Smilacina racemosa* (L.) Desf. var. *amplexicaulis* (Nutt.) S. Watson, U. S. Geol. Expl. Fortieth Parallel **5**: 345. 1871; *Unifolium amplexicaule* (Nutt.) E. Greene, Bull. Torrey Bot. Club **15**: 287. 1888; *Vagnera amplexicaulis* (Nutt.) E. Greene, Man. Bot. San Francisco, 316. 1894. TYPE: United States, [Washington?,] Columbia River Woods, Nuttall s.n. (lectotype, here chosen, GH!).

Vagnera pallescens E. Greene, Proc. Acad. Nat. Sci. Philadelphia **1895**: 551. 1896. TYPE: no specimen cited, type not determined.

Smilacina racemosa (L.) Desf. var. *brachystyla* G. Henderson, Bull. Torrey Bot. Club **27**: 357. 1900. TYPE: United States, Washington, Yakima Co., moist banks of upper MacKenzie River, 13 June 1892, Henderson 4843 (holotype, GH!).

Vagnera brachypetala Rydb. Bull. Torrey Bot. Club **28**: 268. 1901. TYPE: Canada, British Columbia, Glacier at the "Loup," Aug. 1897, Van Brunt s.n. (holotype, NY).

Smilacina amplexicaulis Nutt. var. *glabra* Macbr. Contr. Gray Herb. n.s. **56**: 18. 1918; *Smilacina racemosa* (L.) Desf. var. *glabra* (Macbr.) St. John, Contr. Bot. State Coll. Wash. **20**: 97. 1929; *Vagnera amplexicaulis* (Nutt.) E. Greene var. *glabra* (Macbr.) Abrams, Ill. Fl. Pacific States **1**: 453. 1923. TYPE: United States, California, Tulare Co., South Fork of Raweah River, 22 July 1904, Culbertson 4252 (holotype, GH!).

Smilacina amplexicaulis Nutt. var. *jenkinsii* B. Boivin, Canad. Field-Naturalist **65**: 14. 1951; *Smilacina racemosa* (L.) Desf. var. *jenkinsii* (B. Boivin) B. Boivin, Phytologia **42**: 16. 1979 (including *S. amplexicaulis* var. *ovata*). TYPE: Canada, Alberta, Beaverlodge, Saskatoon Mtn., 26 June 1949, Jenkins 730a (holotype, DAO!).

Smilacina amplexicaulis Nutt. var. *ovata* B. Boivin, Canad. Field-Naturalist **65**: 15. 1951. TYPE: Canada, Saskatchewan, Cypress Hills, aspen woods, 3700 ft, 2 Aug. 1947, Breitung 5241 (holotype, DAO!).

Terrestrial forest herb, 0.75–1.25 m tall. Leafy stem simple, stiff, upright, 75–125 cm long. Leaves clasping, sessile; blade with the apex acute, tip extending less than 2 mm, the base rounded, the surfaces pubescent, rarely glabrous. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Common and abundant in forests and open woodlands; sea level to 700 m alt. in Northwest, over 3000 m alt. in Chihuahua Range in northern Mexico. Shoots produced annually; flowering May–June; fruits retained through September or October.

Like its eastern counterpart, *Maianthemum racemosum* subsp. *amplexicaule* has broad ecological amplitude, reflected in wide latitudinal distribution. East-

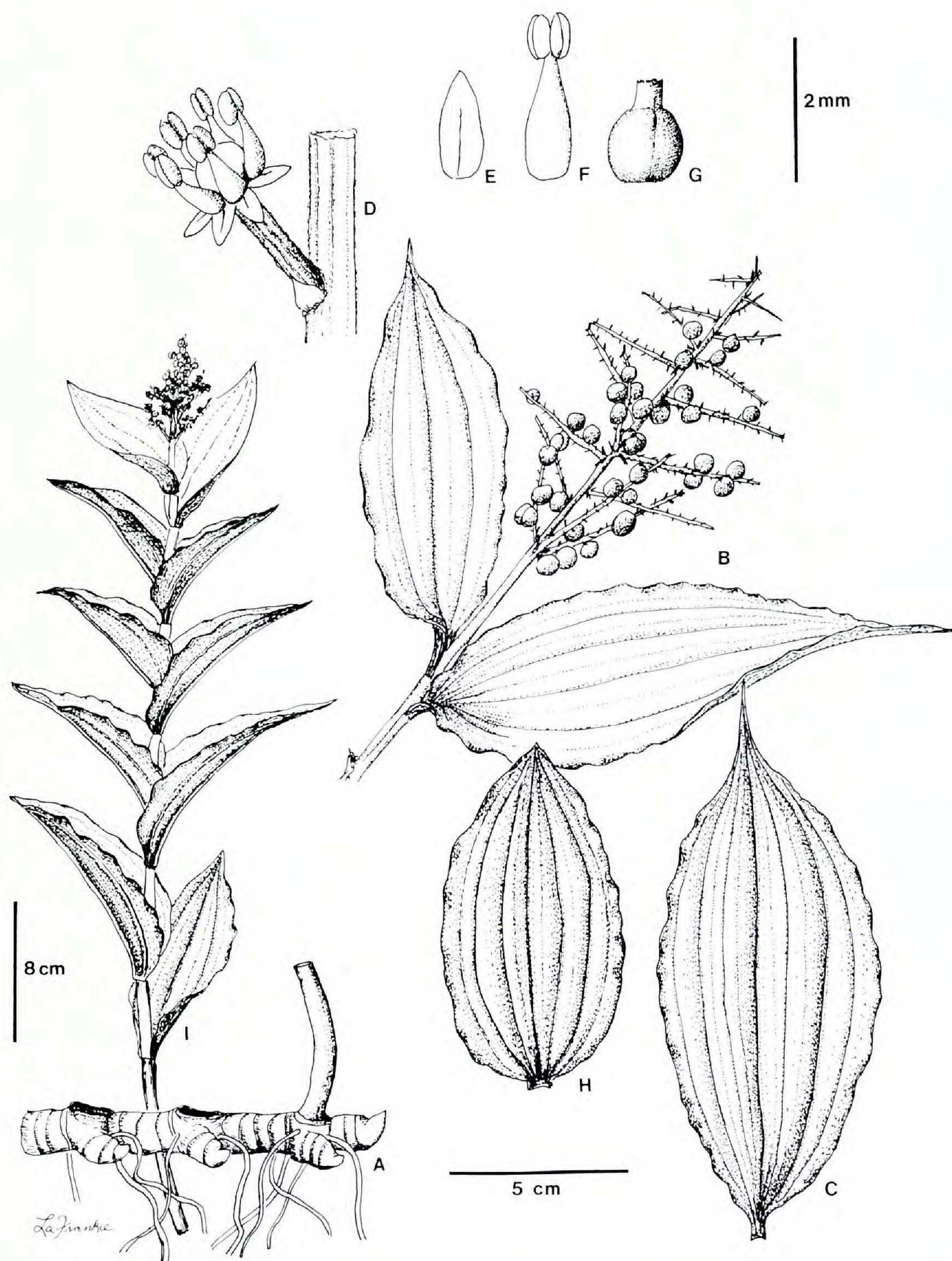
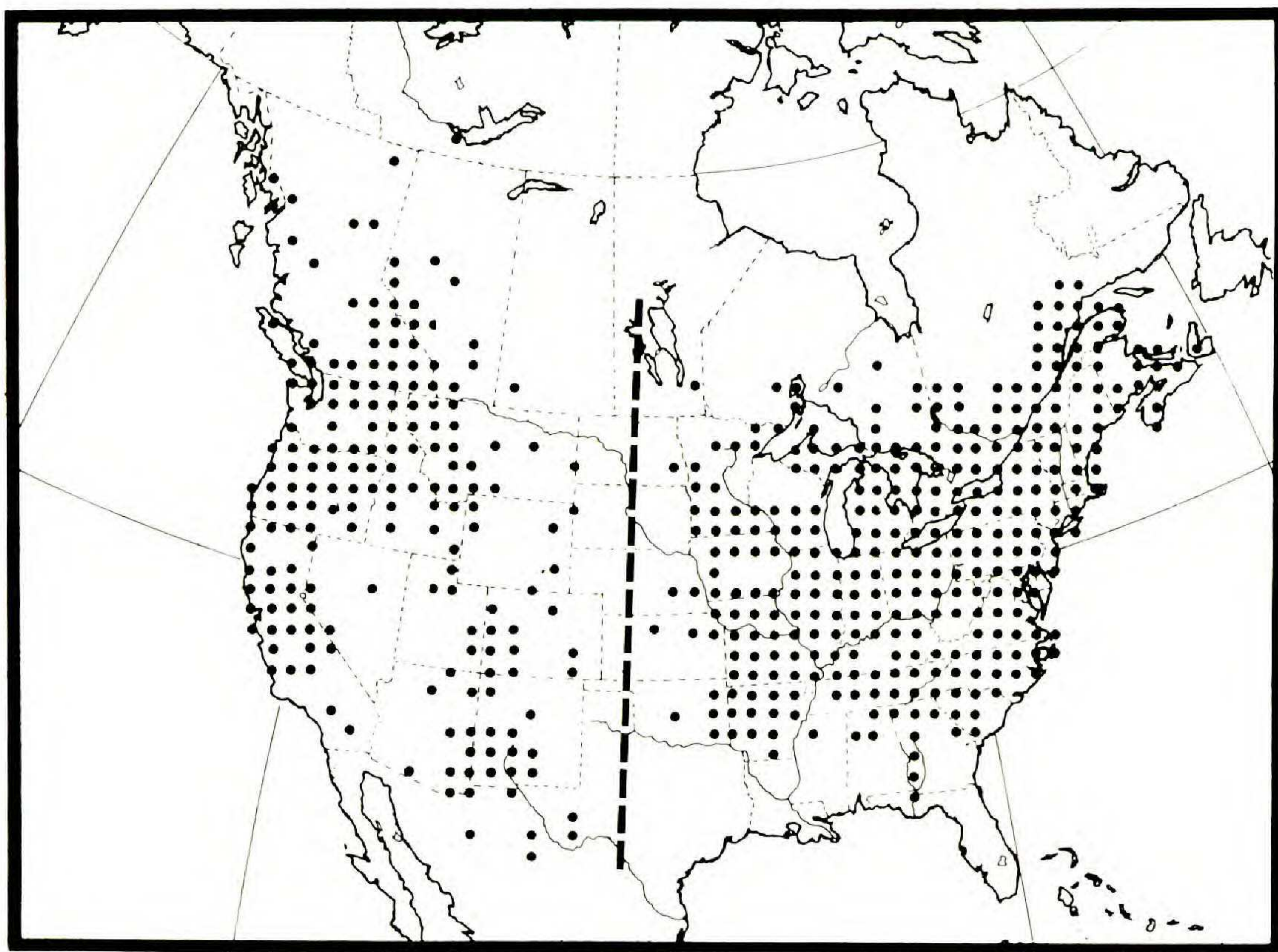


FIGURE 15. *Maianthemum racemosum*. A–G, subsp. *racemosum*: A, rhizome, renewal shoot right, abscission scars of old shoots left; B, upper portion of leafy shoot and infructescence; C, third leaf below inflorescence, showing attenuate-acuminate apex and tapered base; D, flower; E, tepal; F, stamen; G, gynoecium. H, I, subsp. *amplexicaule*: H, third leaf below inflorescence, showing acute apex and rounded base; I, leafy shoot, showing clasping leaves. (A, B, D–G based on *LaFrankie 82-VII-24A* (GH); C on TRT no. 133604, TRT; H on *Smith & Wang 48*, GH.)



MAP 7. Distribution of *Maianthemum racemosum*. Dashed line divides eastern subspecies (subsp. *racemosum*) from western (subsp. *amplexicaule*).

ern limit in foothills of Rockies, from Saskatchewan (Cypress Hills Park, *MacLean s.n.* (GH, PH)) south through Colorado (Mesa Co., 10–12 mi SW of Glade Park, *Pennell 22104* (GH)) and New Mexico (Otero Co., Sacramento Mtns., *Worthington 6215* (LL)) to Texas (Jeff Davis Co., Mt. Livermore, *Hinckley s.n.* (GH, LL)). Southern limit includes some outlying locations in Mexico (Chihuahua, Río de Bavispe, *S. White 3283* (US); Sierra Madre, *Pringle 8036* (GH, MEXU, US)) and extends to southern California (San Bernardino Co., San Bernardino Mtns., below Bear Valley Dam, *Ewan 2756* (CAS)), but species differs from *M. stellatum* in being largely absent from Great Basin. Northern limit from central Alberta (Jasper Park, *Moss 4650* (GH, WS)) to lower coast of Alaska, with few outlying locations in northern British Columbia (Wicked R., near Peace R., *Raup 4235* (CAN, GH)). Western limit in Coast Ranges of Pacific shore.

The western subspecies of *Maianthemum racemosum* is distinguishable from the eastern subspecies by its upright habit, clasping leaves, and short-acute leaf apex; these differences can be seen in the color photographs in Rickett (1966, *pl.* 6; 1972, *pl.* 8). Some plants intermediate between the two subspecies are found in the region between southeastern British Columbia and northern Idaho. There are only a few chromosome counts available for subsp. *amplexicaule*, but all report a diploid number of 36, indicating that this subspecies may have a more stable karyotype than does the eastern subspecies.

10b. *Maianthemum racemosum* subsp. *racemosum* FIGURE 15A–G, MAP 7.

Convallaria racemosa L. Sp. Pl. 315. 1753; *Tovaria racemosa* (L.) Necker ex Baker, J. Linn. Soc., Bot. 14: 565. 1875; *Polygonastrum racemosum* (L.) Moench, Methodus, 637. 1794; *Unifolium racemosum* (L.) Britton, Trans. New York Acad. Sci. 8: 74. 1889; *Vagnera racemosa* (L.) Morong, Mem. Torrey Bot. Club 5: 114. 1894; *Smilacina racemosa* (L.) Desf. var. *typica* Fern. Rhodora 40: 406. 1938. TYPE: [United States, Virginia?,] collector and number not known (lectotype, BM; photograph in Rhodora 40: pl. 512. 1938).

Smilacina ciliata Desf. Ann. Mus. Natl. Hist. Nat. 9: 53. t. 9. 1807; *Convallaria ciliata* (Desf.) Poiret, Encycl., Suppl. 4: 30. 1816. TYPE: not determined.

Smilacina flexicaulis Wender. Schriften Ges. Beförd. Gesamnten Naturwiss. Marburg 2: 249. 1839. TYPE: [origin not known; cultivated in the Botanical Garden, Marburg] (lectotype, here chosen, protologue).

Vagnera retusa Raf. Autik. Bot. 68. 1840. TYPE: Allegheny Mtns., *Rafinesque s.n.* (holotype, PH?, probably destroyed; lectotype, here chosen, protologue).

Vagnera australis Rydb. in Small, Fl. S. E. United States, 270. 1903. TYPE: United States, Alabama, Auburn, 22 April 1896, *Earle & Underwood s.n.* (holotype, NY!).

Smilacina racemosa (L.) Desf. f. *foliosa* Marie-Vict. Contr. Lab. Bot. Univ. Montréal 14: 15. 1929. TYPE: Canada, Québec, environs de Québec, Aug. 1922, *Victorin 16009* (holotype, MT!).

Smilacina racemosa (L.) Desf. var. *cylindrata* Fern. Rhodora 40: 406. 1938. TYPE: United States, Virginia, Princess Anne Co., Little Neck, dry mixed woods, 8, 9 Aug. 1934, *Fernald & Long 3859* (holotype, GH!; isotype, PH!).

Smilacina racemosa (L.) Desf. var. *lanceolata* B. Boivin, Canad. Field-Naturalist 65: 15. 1961. TYPE: Canada, Ontario, Carleton, Junction Gore, railroad embankment, 30 May 1939, *Minshall 74* (holotype, DAO).

Terrestrial forest herb, 0.75–1.25 m tall. Leafy stem arching, thus presenting foliage leaves in horizontal plane, 75–100 cm long. Leaves with petiole 2–6 mm long; blade with the apex long-caudate, 12–28 mm long, the base rounded or tapered, the surfaces pubescent, more densely so abaxially. Chromosome number $2n = 36, 72, 144$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Common and abundant throughout deciduous forests of eastern United States; broad tolerance with regard to water, temperature, and light (Curtis, 1959); in wet, mucky, seasonally inundated forests and river bottoms, and in dry oak-pine forests; generally restricted to deciduous or semideciduous woods, becoming most abundant along borders and light-gaps.

Eastern limit from New Brunswick (York Co., Douglas, *Roberts 59-455* (CAN)) and Nova Scotia (Lunenburg Co., Bridgewater, *Fernald & Long 23650* (GH)) south through South Carolina (Charleston Co., *Moldenke 1195a* (PH)) to mountains of Georgia (Clark Co., Ocone Heights, *Miller 2329* (PH); Bartow Co., Boston Creek, *Forman G31* (PH); Early Co., above Chattahoochee R. near Hilton, *Thorne & Muenscher 2929* (GH)) and site in Florida (Gadsden Co., below River Junction, W side St. Road 269, S of Flat Creek, *Gholson & Baker s.n.* (voucher 10855, "Flora of Florida," FTG)). Southern limit extending west through north-central Alabama (Winston Co., near Franklin Co. line, 14 mi ENE of Haleyville, *Iltis 20190* (WIS); Clay Co., Talladega Natl. Forest, *Whetstone 9930* (GH)), to northern Mississippi (Monroe Co., 6 mi NW of Amory,

Schuster 38246 (DUKE)), with single site in northern Louisiana (Claiborne Parish, ca. 3 mi E of Summerfield, *Thieret 24686* (USL)). Northern range limited by boreal spruce-fir forest; growing along rivers in deciduous coves and alder thickets, yielding oddly scattered distribution from Québec (Timiskaming Co., Ville Marie, lakeshore, *Baldwin & Breitung 4420* (CAN)) west through Ontario (Mt. Chemines, *Tynell 4907* (WAT)) to southern Manitoba. Western range extending into prairies wherever river-bottoms forested and as far south as Oklahoma (Adair Co., 1 mi W of St. Road 51 and U. S. Highway 59, *Perino & Pierson 180* (LL); Delaware Co., Dripping Springs, *Wallis 5586* (LL); Leflore Co., S of Big Cedar, *Correll 34361* (LL)).

Fernald (1938) satisfactorily lectotypified *Maianthemum racemosum* on one of two specimens in the Clifford Herbarium at the British Museum (Natural History) and published a photograph of the lectotype. Fernald did not see the specimen of *M. racemosum* at LINN, which is annotated by Linnaeus (the specimens at BM are not), but it is very much like the specimen at BM. Linnaeus had no doubt been familiar with the species for some time; it had been cultivated in Europe since the seventeenth century (Aiton, 1814), and in 1737 he had described it in his *Hortus Cliffortianus*. The material on which Desfontaines based the name *Smilacina ciliata* was cultivated in Paris, and a specimen may still be in Desfontaines's herbarium, which was transferred to FI. The illustration and description do not indicate any significant difference from *M. racemosum*.

Despite the many specific, varietal, and form names provided for the subspecies, it is quite uniform in significant characters, and I have followed Galway (1945) in reducing all the varietal names to synonymy. This morphological constancy is more remarkable in light of the wide geographic range of *Maianthemum racemosum* and the relatively greater morphological variation exhibited by other species of *Maianthemum*, especially those of the tropical mountains.

The eastern subspecies is obligately apomictic (Gorham, 1953) and cytologically diverse (Kawano & Iltis, 1966). In all of the populations of the eastern United States that I have examined, the seeds are polyembryonic, which further indicates widespread apomixis.

11. *Maianthemum salvinii* (Baker) LaFrankie, *Taxon* **35**: 588. 1986.

FIGURE 16, MAP 6.

Tovaria salvinii Baker, J. Linn. Soc., Bot. **14**: 568. 1875; *Smilacina salvinii* (Baker) Hemsley, Biol. Cent.-Amer., Bot. **3**: 368. 1884; *Vagnera salvinii* (Baker) Standley, J. Wash. Acad. Sci. **15**: 457. 1925; *Smilacina amoena* H. L. Wendl. var. *salvinii* (Baker) Emons, Ann. Missouri Bot. Gard. **32**: 404. 1945. TYPE: Guatemala, Volcán de Atitlán, 9000 ft, *Salvin s.n.* (holotype, K!).

Epiphytic herb, 0.75–1 m tall. Roots uniform, length not known, ca. 2 mm broad, distribution not known. Rhizome not seen. Leafy stem straight or arching, ca. 1 m long, ca. 5 mm broad at midlength, ribbed, glabrous; foliage leaves more than 7; internodes 2–4 cm long, shorter apically. Leaves with petiole 2–5 mm long; blade elliptic to lanceolate, 15–23 by 5–7.5 cm, the apex acuminate, the base rounded or long-tapered, the margin flat, entire, the veins ranked, the

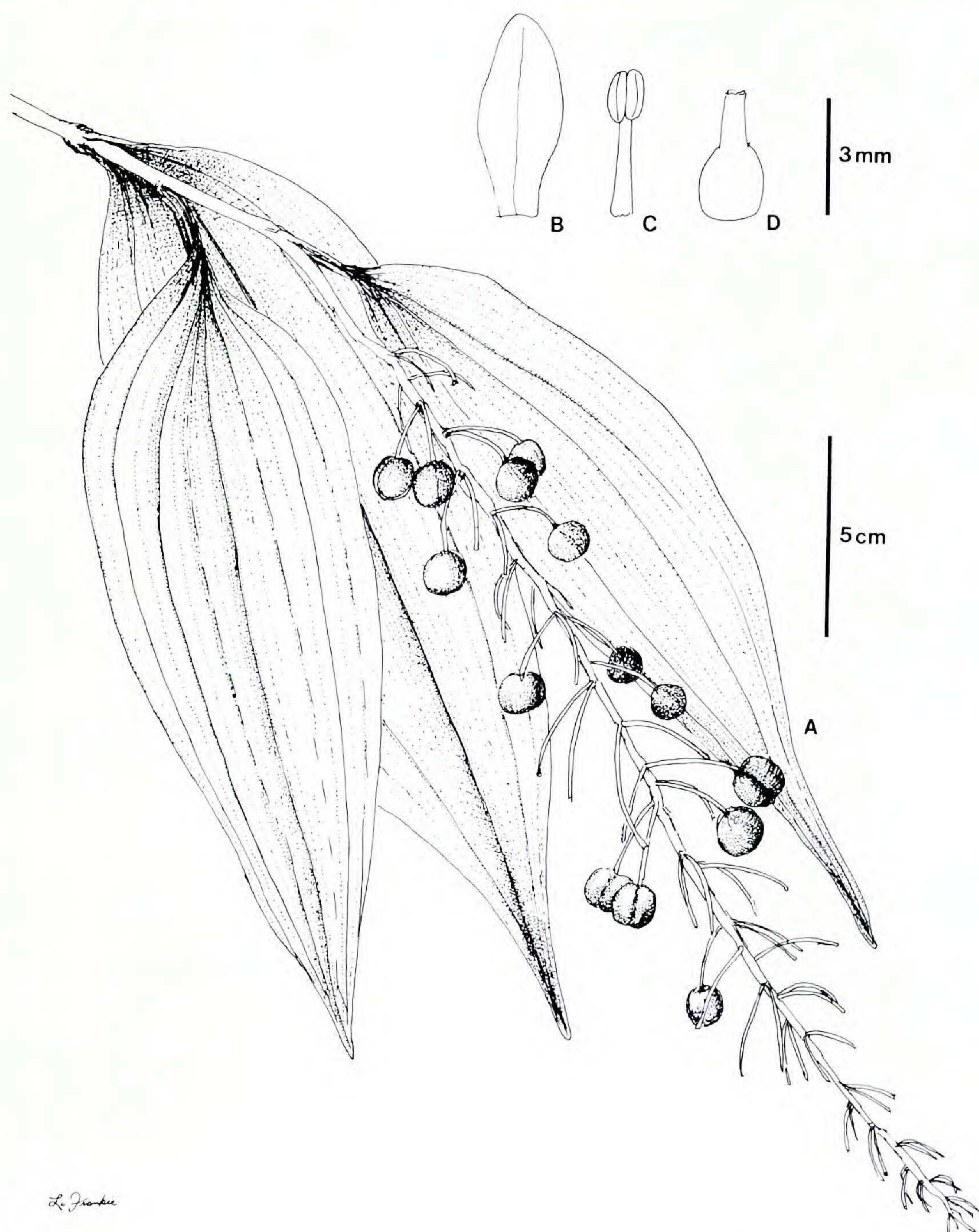


FIGURE 16. *Maianthemum salvinii*: A, upper portion of leafy shoot and infructescence; B, tepal; C, stamen; D, gynoecium. (A based on *Standley* 85045, F; B–D on *Standley* 68691, F.)

surfaces glabrous. Inflorescence a complex raceme with 120 to 150 flowers; main axis pendent, straight, 14–35 cm long, 1.3–2 mm broad at base, ribbed, color not known, glabrous; internodes 25 to 40, most ca. 5 cm long; fascicles arranged in helix, with 3 or 4 flowers, slightly reflexed and drooping, bract subtending each fascicle. Flowers trimerous; pedicel 15–25(–30) by 0.5–0.8 mm, ribbed, glabrous, with bract subtending; perianth cupuliform, the tepals uniform, spreading, 4–4.5 by 2–2.5 mm, pale pink to lavender; stamens inserted

at tepal base, the filament ca. 2 mm long, thin, the anther 0.5–1.1 mm long; ovary spherical, ca. 1 mm in diameter, style 1.5–2 mm long, stigma obscure. Fruits spherical, 8–10 mm in diameter, red at maturity; seeds 3 to 12, oblong, ca. 3 by 2 mm. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Very rare, possibly extinct; primary forests on white sand slopes; 1800–2200 m alt. Flowering in March; fruits retained through January or February.

Endemic to Guatemala.

SPECIMENS EXAMINED. **Guatemala.** SAN MARCOS: Barranca Eminencia, above San Rafael Pie de la Cuesta, 2100–2400 m, *Standley 68691* (F); near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, 1800–2400 m, *L. O. Williams 25685* (F). QUEZALTENANGO: El Pocito, S of San Martín, Chile Verde, 2200 m, *Standley 85045* (F); above Mujulia, S of San Martín, Chile Verde, 1800 m, *Standley 85497* (F).

Maianthemum salvinii was not recognized as a distinct species by Emons (1945). Standley annotated two of the specimens listed above as *Smilacina flexuosa* and one as *S. paniculata*. Emons annotated only one of the specimens, listing it as the hybrid *S. flexuosa* × *amoena*. The four specimens are distinguished from all other species in Central America in having long, strictly racemose inflorescences, long pedicels, and large, cupuliform, rose-colored flowers. With these flowers and the large, pendent inflorescence, *Maianthemum salvinii* is possibly the most spectacular of the Central American species of *Maianthemum*.

12. ***Maianthemum scilloideum*** (M. Martens & Galeotti) LaFrankie, *Taxon* **35**: 588. 1986. FIGURE 17, MAP 8.

Smilacina scilloidea M. Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles* **9**: 388. 1842; *Tovaria scilloides* (M. Martens & Galeotti) Baker, *J. Linn. Soc., Bot.* **14**: 567. 1875. TYPE: Mexico, Oaxaca, Cerro San Felipe, *Galeotti 5471* (lectotype, here chosen, BR (BR no. 3394-84-9!); isoelectotypes, BR (BR nos. 3394/84-8! and 3394/84-10!), K!).

Smilacina scilloidea M. Martens & Galeotti var. *acutifolia* M. Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles* **9**: 388. 1842. TYPE: Mexico, Oaxaca, [Sierra Madre Oriental,] Cordillera Oriental, *Galeotti 5483* (not *Galeotti 5471* as in protologue) (lectotype, here chosen, BR (BR no. 3394/84-12!); isoelectotypes, BR (BR no. 3394/84-11!), K!, NY!, US!).

Smilacina scilloidea M. Martens & Galeotti var. *rosea* Emons, *Ann. Missouri Bot. Gard.* **32**: 406. 1945. TYPE: Guatemala, Volcán Santa María, *Skutch 869* (holotype, F!; isotype, US!).

Terrestrial forest herb, 15–35 cm tall. Roots uniform, 15 to 35 per rhizome unit, at nodes and internodes, mostly clumped near base of leafy shoot, 10–15 cm by 0.5–1 mm. Rhizome a long sympodium, forking, spreading widely, the individual units narrow-cylindrical, 5–10 cm by 4–8 mm, slightly flattened, the scale leaves 8 or 9, the internodes 6–14 mm long, shorter distally and apically, the lateral buds 5 or 6, axillary, 1 or 2 (rarely 3) developing as leafy shoots; epidermis replaced by periderm; starch only near rhizome apex. Leafy stem upright, 15–30 cm long, 3–4 mm broad at base, surface smooth or ribbed,

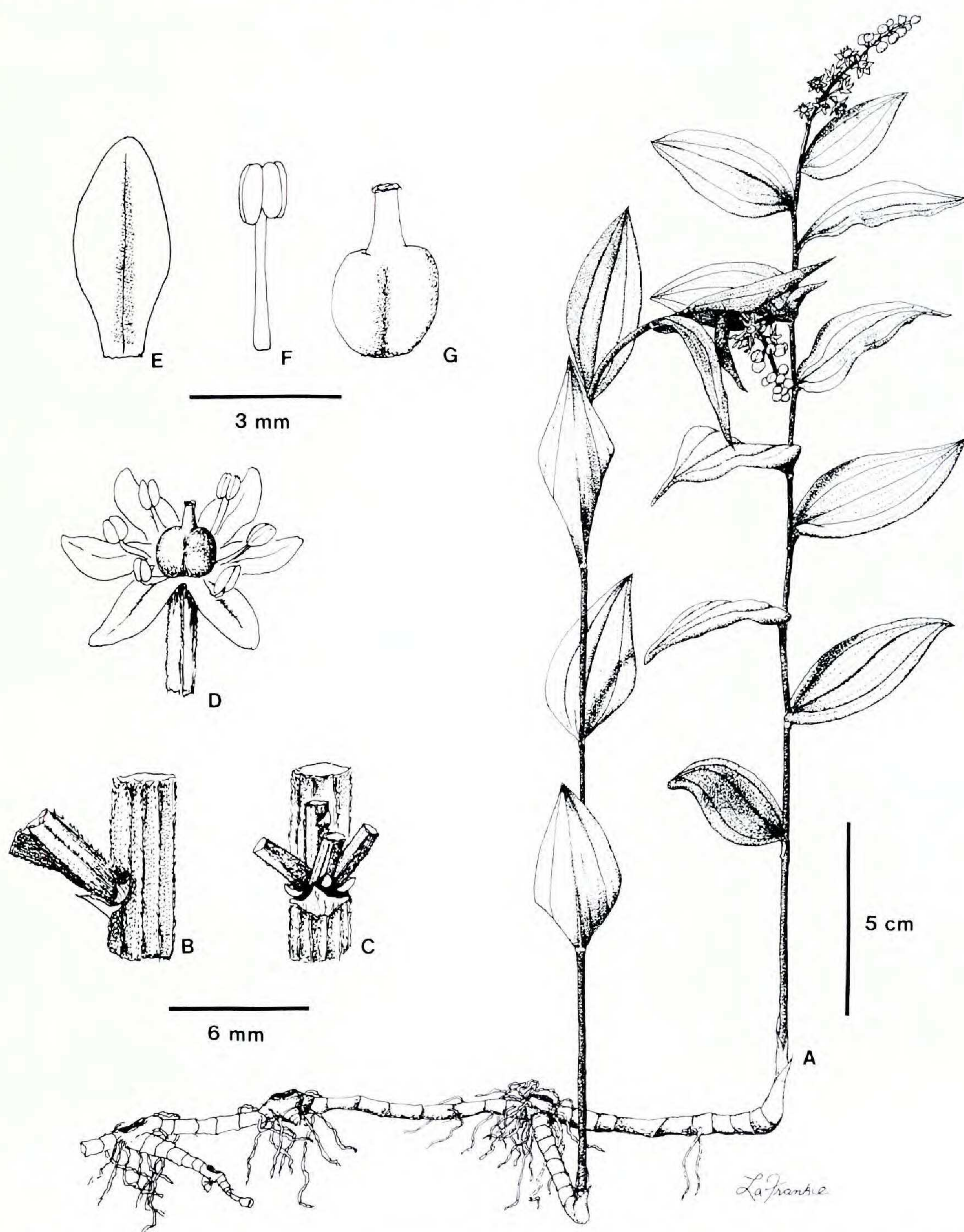
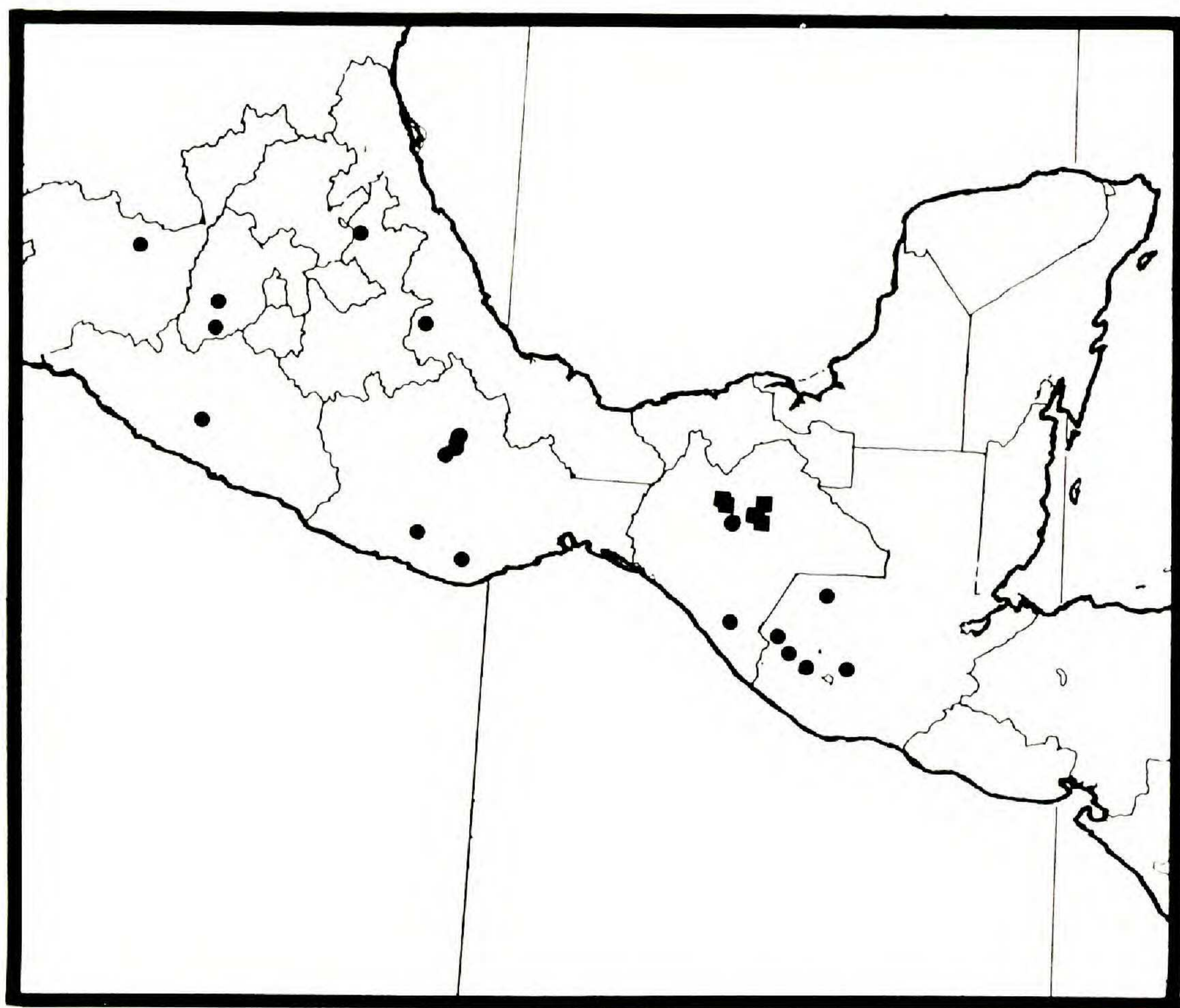


FIGURE 17. *Maianthemum scilloideum* (LaFrankie 83-IV-24A, GH): A, rhizome, leafy shoot, and inflorescence; B, C, lateral fascicles of inflorescence, showing 2 and 4 pedicels; D, flower; E, tepal; F, stamen; G, gynoecium.

glabrous; foliage leaves 6 to 9; internodes 2.5–5 cm long, shorter apically. Leaves sessile and clasping, or with petiole 2–3 mm long; blade elliptic to ovate, 5–8 by 2–3.5 cm, the apex short-acuminate, the base rounded, the margin flat, with denticles distinct, the veins ranked, the surfaces glabrous. Inflorescence a complex raceme with 8 to 27 flowers; main axis drooping at first, upright when



MAP 8. Distribution of *Maianthemum scilloideum* (dots) and *M. septifolium* (squares).

mature, straight, 1.5–4 cm long, 1–1.5 mm broad at base, ribbed, green or maroon, glabrous or sometimes with denticles; internodes 4 to 8, 2–7 mm long; fascicles arranged in helix, with 2 or 3 (or 4) flowers, spreading, with bract subtending each fascicle. Flowers trimerous; pedicel 3.5–8 by 0.4–0.6 mm, ribbed, glabrous or rarely with denticles, with bract subtending; tepals uniform, spreading, 3–6 by 1–1.5 mm, white; stamens inserted at tepal base, the filament 1–1.5 mm long, thin, the anther 0.5–1 mm long; ovary cylindrical, 1–1.8 by 1 mm, the style ca. 1 mm long, the stigma 3-lobed, 0.3–0.4 mm broad. Fruits spherical, 6–8 mm in diameter, green when young, maturing to red; seeds 1 to 3, spherical, 4–5 mm in diameter. Chromosome number not known.

ECOLOGY AND DISTRIBUTION. Clonal, forming loose, spreading patches in understory of conifer-oak forests; 1700–3500 m alt. Shoots usually developing on annual cycle; flowering April–August; fruits retained June–December.

Historically, as far to northwest as Michoacán; presently, scattered occurrences in Guerrero and along Pacific coastal ranges, but most common from Sierra de Ixtlán of Oaxaca to the northern highlands of Chiapas, and in scattered alpine sites in Guatemala.

SPECIMENS EXAMINED. **Mexico.** MICHOACÁN: Cerro Azul, *Arsène* 5766 (GH, MO, NY, US); vic. Morelia, *Arsène* 5803 (US). MÉXICO: Temascaltepec, *Hinton* 886 (MICH, NY, UC, US), 4520 (F, GH, NY, US), 5079 (F, NY), 7953 (F, LL, MO, NY, TEX, US), *Matuda* 31991 (MEXU); Galeana, *Hinton* 14227 (GH, MICH, NY, US), 14290 (GH, LL, MO, NY, TEX, US); Yesceros, *Hinton* 14407 (F, GH, LL, NY, TEX, US); 5 km S of Sultepec, *Rzedowski* 30796 (MEXU); Cerro de Pinal, *Matuda* 31888 (MEXU). PUEBLA: W slopes below Puerto-del-Aire, *C. Smith* 3928 (F, MEXU, US); vic. Huauchinango, *Sharp* 45394 (TENN). VERACRUZ: Lom-agrande, vic. Orizaba, *Balls* B4350 (GH, MS, NY, UC, US); Planta el Pie, Chiconquiaco, *Ventura* 7018 (CAS); El Puerto, *Sharp* 44709 (NY, TENN); 3 km NE of Nueva Vaquera, *Calzada* 5917 (XAL); intersection of Rte. 175 and road to Puerto-del-Aire, *Horvitz* 39841 (XAL). OAXACA: Cerro San Felipe, *Galeotti* 5471 (BR), 5483 (BR, NY, US), *Gonzales* 704 (GH, US), *Pringle* 4647 (GH, MEXU, MICH, NY, UC, US); 27 km N of Ixtlán [on Rte. 175], *LaFrankie* 83-30 (GH), *Roe* 1964 (DS, F, MICH, WIS); 25 km N of Ixtlán, *Rzedowski* 30653 (LL, MICH), *Taylor* 2415 (DUKE); 12 km N of Ixtlán, *McPherson* 826 (CAS, MICH); 30 km NE of Oaxaca, *Conrad* 3118 (GH, MO); 7 mi NE of Oaxaca, *Webster* 11508 (GH, MS); vic. Zempoaltepec, *Hallberg* 820 (MEXU, MICH), *E. Nelson* 667 (US); San Miguel, *Reko* 3840 (US); 35 km S of Juchatengo, *Roe* 580 (F, WIS); 21.9 mi S of Suchixtepec, *Croat* 46100 (MEXU); 3 km S of San José del Pacífico, *Ortega* 1767 (XAL). GUERRERO: 4 mi W of Omiltemi, *Wilkinson* 3371 (MEXU, MICH); 3 mi W of Omiltemi, *Hamilton* 3262 (MEXU, MICH); N slope of Cerro Alquitrán, *Anderson* 4446 (MICH); 5 km W of Camotlá, *Sanchez s.n.* (MEXU); 18 km S of Filo de Caballo, *Rodriguez* 85 (MEXU). CHIAPAS: Cerro Huitepec, *Alexander* 1135 (MEXU, MICH, US), *Breedlove* 23023 (DS, MICH, MO, NY), *Laughlin* 1027 (CAS, MEXU, UC, WIS), 1853 (DS); Cerro Zontehuitz, *Breedlove* 6662 (DS, US); Santa Rosa, near Escuintla, *Matuda* 4256 (GH, LL, MEXU, NY); Volcán Tacaná, *Matuda* 2365 (GH, MEXU, MICH). **Guatemala.** HUEHUETENANGO: between San Mateo Ixtatán and Nucá, *Steyermark* 49842 (F, US); vic. Tunima, *Steyermark* 48412 (F, NY, US); Cerro Pixpix, *Steyermark* 50561 (US). QUEZALTENANGO: Volcán Zunil, *Steyermark* 34720 (F, MO); Volcán Santa María, *Skutch* 869 (F, GH, US). SAN MARCOS: 4.4 mi W of Ixchiguan, *Beaman* 3244 (GH, LL, MS, UC, US); between San Marcos and Serchill, *Standley* 85391 (F, US), 85418 (F). CHIMALTENANGO: Volcán Acatenango, *Standley* 61890 (F).

Among the duplicates at BR, one set of specimens evidently received full printed labels and contains handwritten notes by Martens concerning location and floral morphology; I have chosen these as the lectotypes. The duplicates have different labels or none at all, and usually have much-abbreviated label annotations. The type material under this species is all very uniform, unlike the situation with *Maianthemum paniculatum*.

The distinction between *Maianthemum scilloideum* and *M. flexuosum* is presented under the discussion of the latter species. In general, *M. scilloideum* is a diminutive plant of higher mountains, and it is not easily confused with any other species.

13. *Maianthemum septifolium* LaFrankie, sp. nov. FIGURE 18, MAP 8.

A speciebus aliis *Maianthemii* in foliis 6 ad 8 (ad 10), rhizomate angusto, elongato, cylindrico vel leviter complanato, 2–5.5 cm longo, 0.8–1.4 cm lato, inflorescentia plerumque paniculata, petalis 2–4 mm longis, 1.2–2 mm latis, differt.

Terrestrial forest herb, 45–75 cm tall. Roots uniform, 10 to 20 per rhizome unit, scattered at nodes and internodes, 15–35 cm by 1.5–2 mm. Rhizome a dense or spreading, forking sympodium, the individual units narrow-cylindri-

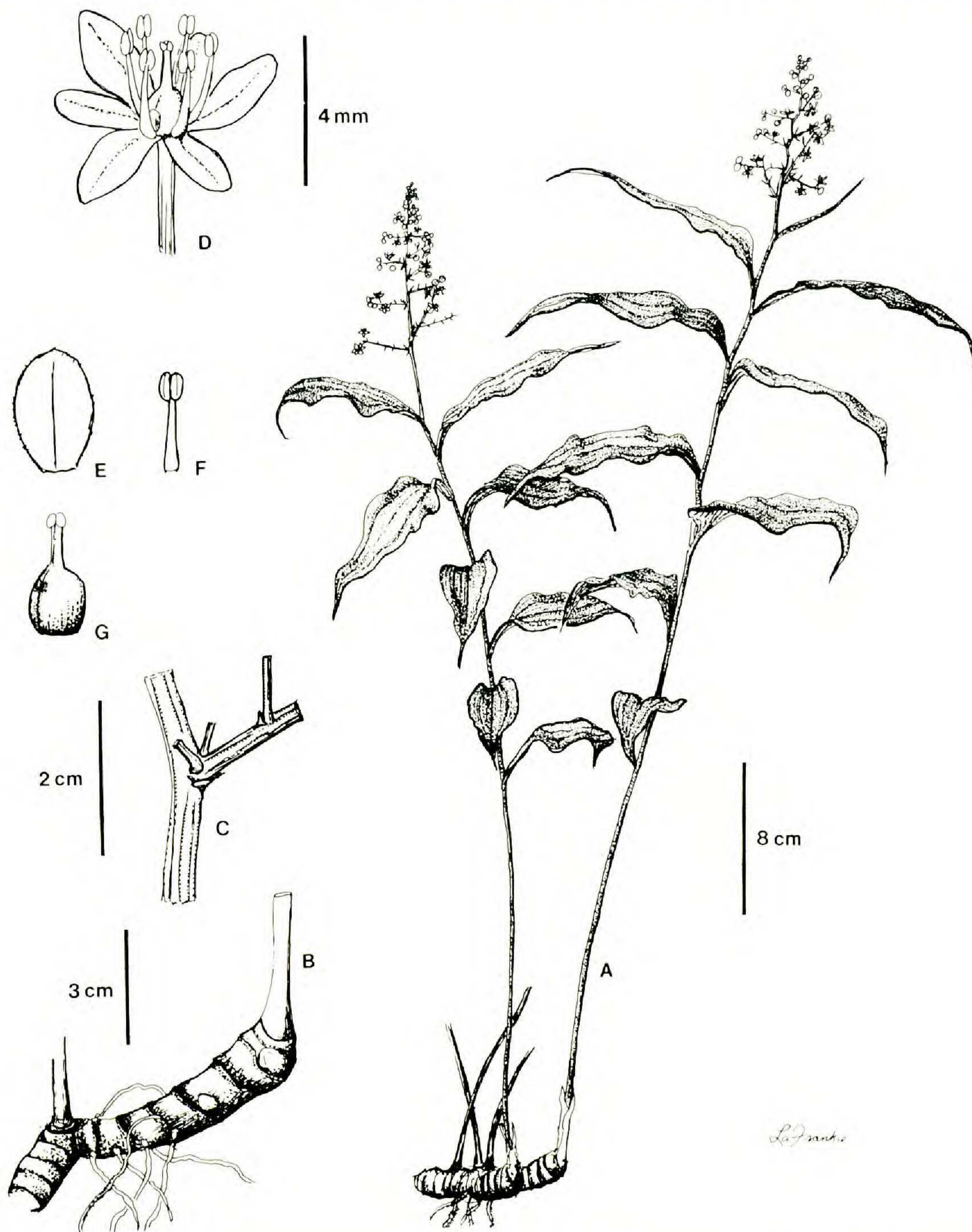


FIGURE 18. *Maianthemum septifolium* (LaFrankie 84-V-19B, GH): A, leafy shoots with inflorescences; B, rhizome; C, lateral branch of inflorescence; D, flower; E, tepal; F, stamen; G, gynoecium.

cal, slightly flattened, 2–5.5 by 0.8–1.4 cm, the scale leaves 7 or 8, the internodes 5–8(–12) mm long, shorter apically, the lateral buds 7, axillary, 1 or 2 developing as leafy shoots; epidermis replaced by periderm; starch more dense distally, but nowhere very dense. Leafy stem stiff, upright, tapering, 35–55 cm long, 2.5–3.5 mm wide at base, the surface smooth, glabrous; foliage leaves 6 to 9 (or 10); internodes 3–5 cm long, shorter apically. Leaves with petiole 5–

9 mm long; blade elliptic, 9–14 by 3.5–5(–7) cm, the apex acuminate, the base tapered, the margin slightly undulate, entire or with denticles near apex, the veins ranked, the surfaces glabrous. Inflorescence a cylindrical panicle with 25 to 60 flowers; main axis upright, stiff, slightly flexuate, 6–8 cm long, 1–1.5 mm wide at base, ribbed, green, glabrous; internodes 8 to 12 (to 15), 4–7 mm long; lateral axes racemes (rarely lower ones dense fascicles), arranged in helix, spreading, 10–25 mm long, with 1 or 2 flowers at base and others at intervals of 1–3(–5) mm, with bract subtending each raceme. Flowers trimerous; pedicel 2–4 by 0.8–1.2 mm, ribbed, glabrous, with bract subtending; tepals more or less uniform, 2–4 by 1.2–2 mm, reflexed to spreading, white; stamens inserted at tepal base, the filament 1.2–1.5 mm long, thin, the anther 1–1.2 mm long; ovary spherical, 1.2–1.5 mm in diameter, the style ca. 1 mm long, the stigma distinctly 3-lobed, 0.6 mm broad. Fruits spherical to weakly 3-lobed, 8 mm broad, green with red spots when young, maturing to red; seeds 1 to 3, spherical, 1–1.5 mm in diameter. Chromosome number $2n = 36$ (*fide* M. S. Cave, voucher *Tillet 636-5* (UC)).

TYPE. Mexico, Chiapas, 9 km S of Rayón, 6 km N of Rincón Chamula, steep hillside, cloud forest, 19 May 1984, *LaFrankie 84-V-19B* (holotype, GH).

ECOLOGY AND DISTRIBUTION. Clonal, forming dense clumps along trails, in broken forest, on steep slopes; 1800–2800 m alt. Flowering January–July; fruits maturing slowly, retained 3–6 months; fruiting and flowering stems sometimes occurring on same individual.

Principally in northern highlands of Chiapas, Mexico.

SPECIMENS EXAMINED. **Mexico.** VERACRUZ: Chicoquiaco, *Ventura 7018* (F). CHIAPAS: vic. Pueblo Nuevo Solistahuacán, *Breedlove 19789* (DS), *19842* (DS, F, LL), *20012* (DS), *Clarke 357* (DS), *Lathrop 5209* (DS), *5816* (DS, MO, US), *Thorne 40310* (DS), *41089* (DS), *Tillet 636-5* (DS, GH, US), *Ton 2801* (DS), *2844* (DS, WIS), *Zuill 59* (DS), *193* (DS); vic. Tenejapa, *Breedlove 10806* (DS, F, MICH, MS, NY, US), *Ton 593* (DS, F, MS, NY, US), *1752* (DS, DUKE, NY, US), *2316* (DUKE, WIS); 2 mi S of Jitotol, *Roe et al. 1187* (F, WIS).

In dimensions *Maianthemum septifolium* is intermediate between *M. scilloideum* and *M. paniculatum*. This is another of the species with paniculate inflorescences that was previously confused with *M. paniculatum*, but it can be distinguished from that species by the smaller stature at which it reaches reproductive maturity. *Maianthemum paniculatum* does not initiate an inflorescence until it has at least ten foliage leaves, then continues to produce larger shoots with as many as 17 leaves. Most plants of *M. septifolium* are quite constant in producing shoots with a maximum of seven leaves; only rare collections have as many as ten.

This species is somewhat unusual in the volume of nectar it exudes from the septal nectaries. A large, clear drop of viscid nectar collects at the tepal junction below each septal pore.

Although it is not a widespread species, I have found *Maianthemum septifolium* to be one of the more hardy and one of the easiest to keep in cultivation. It produces shoots more or less continuously and reaches reproductive size very quickly.

14. ***Maianthemum stellatum* (L.) Link**, Enum. Hort. Berol. Alt. **1**: 343. 1821. FIGURE 19, MAP 9.

Convallaria stellata L. Sp. Pl. 316. 1753; *Tovaria stellata* (L.) Necker ex Baker, J. Linn. Soc., Bot. **14**: 565. 1875; *Smilacina stellata* (L.) Desf. Ann. Mus. Natl. Hist. Nat. **9**: 52. 1807; *Asterantherum vulgare* Kunth, Enum. Pl. **5**: 151. 1821 (nomen illegit.); *Unifolium stellatum* (L.) E. Greene, Bull. Torrey Bot. Club **15**: 287. 1888; *Vagnera stellata* (L.) Morong, Mem. Torrey Bot. Club **5**: 114. 1894; *Asterantherum stellatum* (L.) Niewl. Amer. Midl. Naturalist **3**: 109. 1913. TYPE: probably described from literature (lectotype, here chosen, Cornut, Canad. Pl. *t.* 33. 1635).

Smilacina stellata var. *uniflora* Pursh, Fl. Amer. Sept. **2**: 733. 1814; *Asterantherum vulgare* Kunth var. *uniflora* (Pursh) Kunth (nomen illegit.). TYPE: not determined (but see *Sherard Herbarium* no. 725, OXF).

Vagnera angustifolia Raf. Autik. Bot. 68. 1840. TYPE: United States, near Niagara Falls, *Rafinesque s.n.* (holotype, PH?, probably destroyed; lectotype, here chosen, protologue).

Tovaria sessilifolia Nutt. ex Baker, J. Linn. Soc., Bot. **14**: 566. 1875 (*Smilacina sessilifolia* Nutt. ex Baker, pro syn.); *Unifolium sessilifolium* (Baker) E. Greene, Bull. Torrey Bot. Club **15**: 287. 1888; *Vagnera sessilifolia* (Baker) E. Greene, Man. Bot. San Francisco, 316. 1894; *Smilacina stellata* (L.) Desf. var. *sessilifolia* (Baker) Henderson, Bull. Torrey Bot. Club **27**: 358. 1900. TYPE: United States, Rocky Mtns. and Columbia Woods, [ca. 1835,] *Nuttall s.n.* (lectotype, here chosen, K; isolectotype, PH!).

Unifolium liliaceum E. Greene, Pittonia **1**: 280. 1889; *Vagnera liliacea* (E. Greene) Rydb. Mem. New York Bot. Gard. **1**: 101. 1900; *Smilacina liliacea* (E. Greene) Wynd. Amer. Midl. Naturalist **17**: 902. 1936. TYPE: not determined.

Smilacina stellata (L.) Desf. f. *paniculata* St. John, Proc. Biol. Soc. Wash. **50**: 4. 1937. TYPE: United States, Washington, Silverton, 1899, *Bouck 185*, in part (holotype, WS!).

Vagnera leptopetala Rydb. Bull. Torrey Bot. Club **28**: 268. 1901. TYPE: United States, headwaters of Sangre de Cristo Creek, 1901, *Rydberg & Vreeland 6441* (holotype, NY!).

Vagnera stellata (L.) Morong var. *mollis* Farw. Bull. Torrey Bot. Club **42**: 357. 1915. TYPE: United States, Michigan, Parkdale Farm, 30 May 1914, *Farwell 3651* (holotype, MICH; isotype, GH!).

Smilacina stellata (L.) Desf. var. *crassa* Marie-Vict. Contr. Lab. Bot. Univ. Montréal **14**: 16. 1922. TYPE: Canada, Québec, Île Nue, archipel de Mingan, 29 July 1926, *Victorin & Rolland 24249* (holotype, MT; isotypes, GH!, PH!).

Smilacina stellata (L.) Desf. var. *sylvatica* Marie-Vict. & Rouss. Contr. Lab. Bot. Univ. Montréal **36**: 66. 1940. TYPE: Canada, Québec, Rivière Petite-Cascapédie, 10 April 1930, *Victorin & Rolland 33831* (holotype, MT; isotype, GH!).

Terrestrial herb, 15–45 cm tall. Roots dimorphic, 40 to 150 small ones (0.5–0.7 mm broad) scattered over each rhizome unit, 3 to 6 large ones (0.9–1.2 mm broad) clumped near base of leafy shoot. Rhizome a long-linear sympodium, forking, spreading, the individual units long, narrow-cylindrical, 15–40(–80) cm by 3–4.5 mm, the scale leaves 5 or 6, the 2nd and 3rd internodes 5–25 cm long, others 3–10 mm, the lateral buds 3 or 4, axillary, 2 or 3 developing as leafy shoots; epidermis replaced by densely pilose absorptive layer above distinct hypodermis; starch abundant in rhizome portions 1–2 years old, depleted in older portions. Leafy stem stiff, upright, 25–50 cm long, 2–3.5(–5) mm broad at base, the surface smooth, with denticles; foliage leaves 8 to 11 (to 14); internodes 2–3.5 mm long, shorter apically. Leaves clasping (sometimes

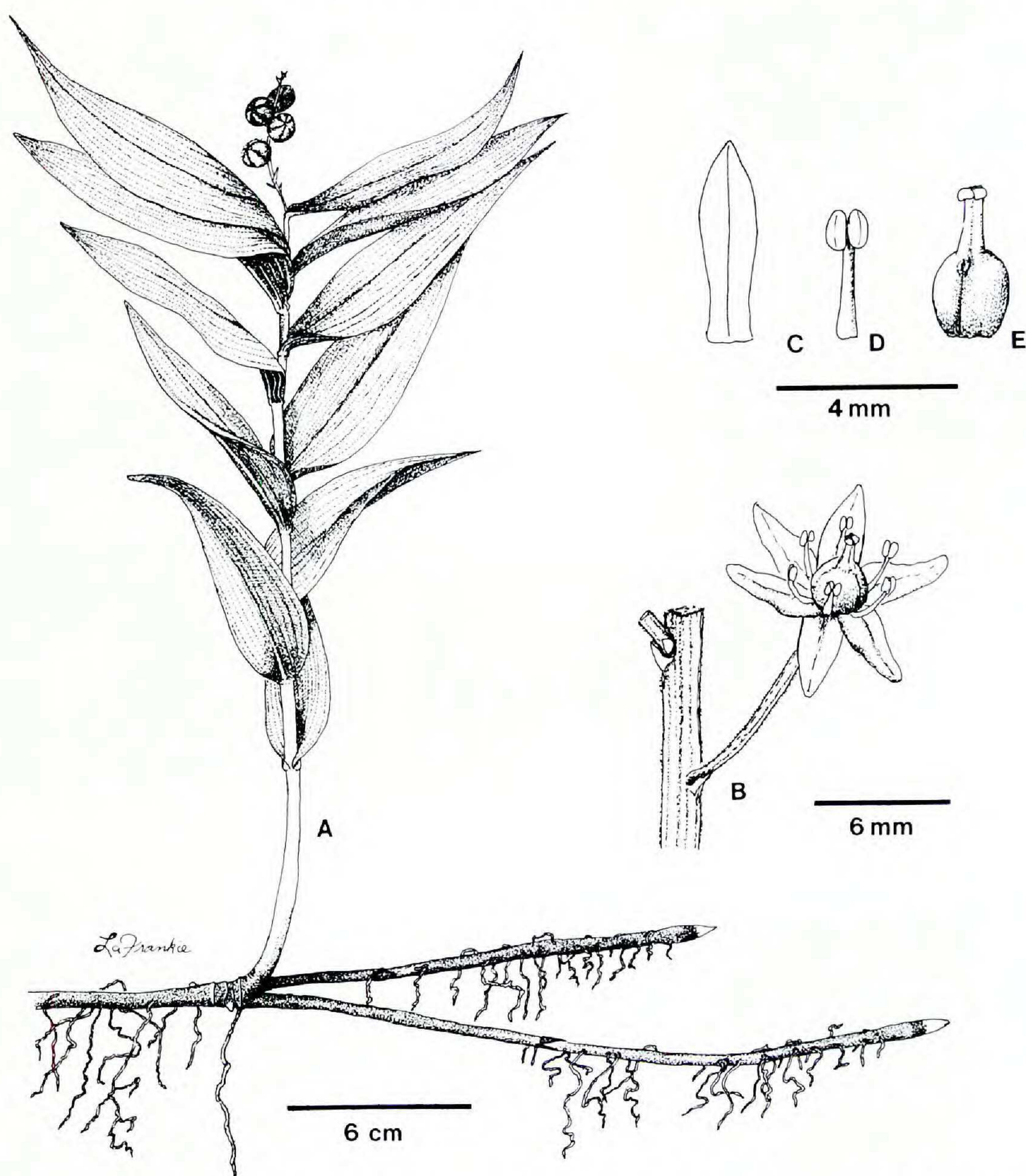
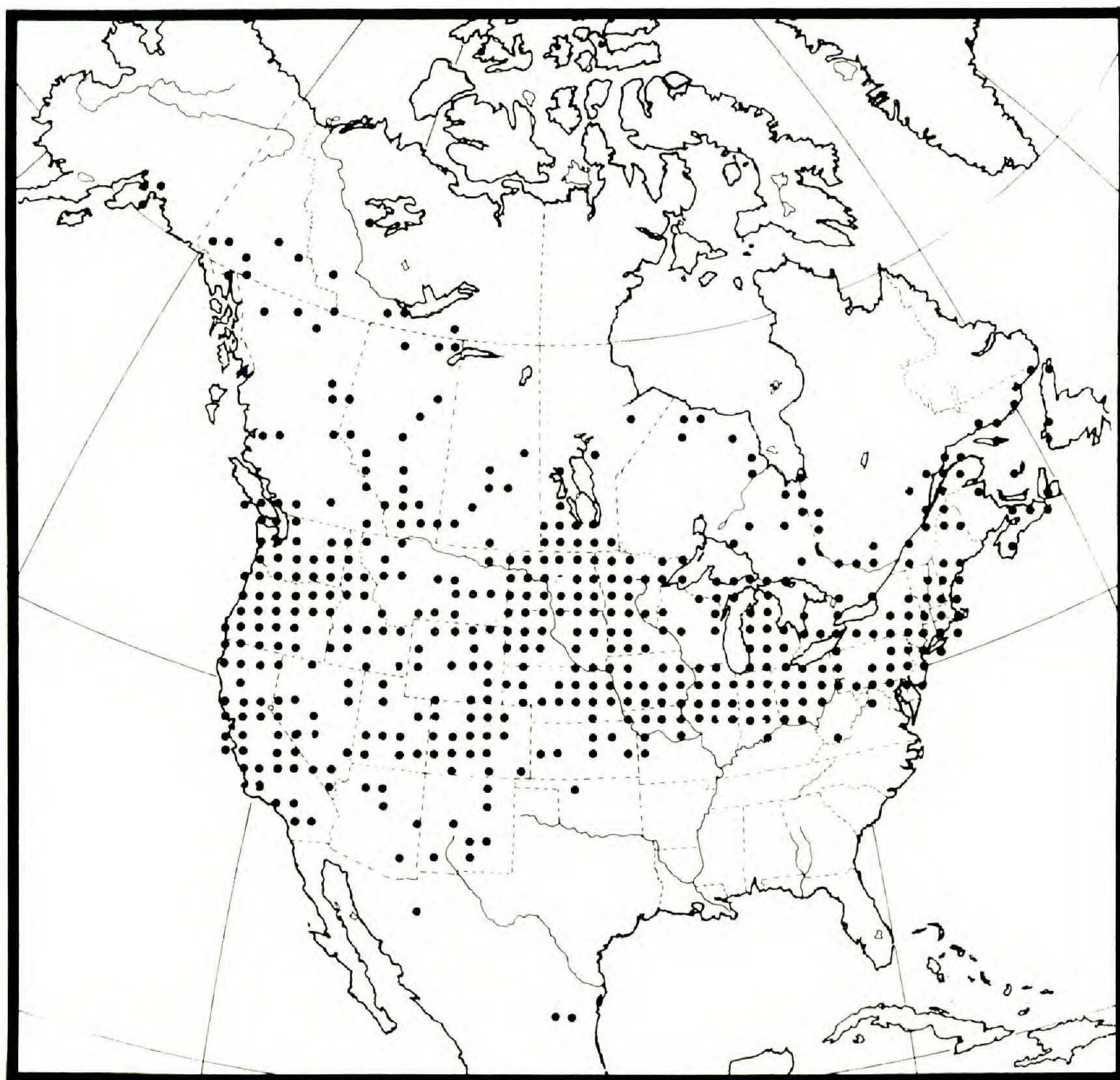


FIGURE 19. *Maianthemum stellatum* (LaFrankie 76, GH): A, rhizome, leafy shoot, and infructescence; B, flower; C, tepal; D, stamen; E, gynoecium.

short-petiolate in western United States); blade ovate-elliptic to lanceolate, 5–6(–10) by 2.5–3.5(–5.5) cm, the apex acute, the base rounded, the margin flat, with denticles very distinct and pointed forward, the veins of uniform strength or weakly ranked, the surfaces usually pubescent. Inflorescence a simple raceme with 6 to 15 flowers; main axis upright, straight or slightly flexuous, 4–5.5 cm long, 0.5–1.5 mm broad at base, ribbed, green, pubescent; internodes 3–8 mm long; flowers arranged in helix. Flowers trimerous; pedicel arched-ascending, ribbed, usually pubescent or denticulate, with 1 bract subtending, usually an additional 1 at pedicel base or at midlength; tepals uniform, spreading, 4–5 by 1.5–2 mm, white; stamens inserted at tepal base, the filament 1.2–1.5 mm long, thin, the anther 0.6–0.8 mm long; ovary spherical to cylindrical, ca. 1



MAP 9. Distribution of *Maianthemum stellatum*.

mm broad, style 1.3–1.8 mm long, stigma obscurely 3-lobed. Fruits spherical, 4–6 mm in diameter, green with black stripe along each median carpel vein when young, maturing to red; seeds 1 to 6, spherical, 2.5–3 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Clonal, with scattered occurrence throughout much of range, although in some habitats abundant to subdominant; generally in wet sites with periodic edaphic disturbance. Flowering April–June; fruits retained through September.

Very common in sand dunes of Atlantic coast from New Brunswick to New Jersey, inland along river shores, creek banks, sand dunes, gravel and sand washes of prairies; in American Midwest and Far West more frequently in marginal woodland habitats and oak-pine openings, especially above 1000 m.

Eastern limit extending from Newfoundland (Northumberland Co., Fox Is., *Blake* 5687 (LL)) and Nova Scotia (Cape Breton Is., Bird Is., *Nichols* 588 (GH)) south along coast through New Jersey (Cape May Co., 1 mi S of Peermont, *Fender* 1369 (GH)). Inland, southern limit occurring through mountains of

Virginia (Giles Co., along Rte. 100, ca. 10 mi S of Pearisburg, *Nicely s.n.*, 19 May 1961 (WVA)) and West Virginia (Summers Co., river bank near Bellpoint, *Boone 194* (WVA)) west through single location in Kentucky (Lewis Co., along Chalk Ridge Road, ca. 6 mi N of Tollesboro, *Thieret 53617* (KNK)), through Posey Co., Indiana (Deam, 1940), and Illinois (Monard Co., *E. Hall s.n.* (PH); Wabash Co. (Mohlenbrock & Ladd, 1978)) to Missouri (Shelby Co., Shelbina, *Palmer 40852* (GH); Shannon Co. (Steyermark, 1963)) and Oklahoma (Woodward Co., Boiling Springs State Park, *Goodman 7303* (GH)). Northern limit extending from Québec (S shore James Bay, Île Lemoine, *Dutilly 14-083* (GH)) to Manitoba (Hayes R., opposite mouth of Fox R., *Scoggan 5859* (GH)) to Northwest Territories (MacKenzie Distr., Salt Plain, W of Fort Smith, *Cody 3788* (LL)) and Yukon Territory (Whitehorse, *Calder 2863* (CAS); Ross R., Pelly R., upper terrace, *Denniston 25* (WIS)). In West, exhibiting remarkable latitudinal range, from Alaska (Chugach Mtns., middle slope, near Lake Eklutna, *York B205* (LL)) south through Rocky Mtns. and California ranges, here occurring at both low (San Mateo Co., San Andreas Lake, ca. 200 m, *Baker 1915* (GH, LL)) and high (Mono Co., Harvey Monroe Hall Natural Area, 3230 m, *Clausen 1636* (UC)) elevations, south to southern California (Riverside Co., San Gabriel Mtns., Strawberry Valley, *Grant s.n.* (CAS); Los Angeles Co., San Gabriel Mtns., Dawson Saddle, *Griesel s.n.* (DS)) and through Southwest to Nevada (Clark Co., Charleston Park, *Clokey 7879* (CAS, GH, US, WIS)) and northern Mexico (Chihuahua, near Colonia Garcia in Sierra Madre, 7500 ft, *Townsend & Barber 35* (F, MO, NY, UC, US)), widely disjunct in highest peaks of Nuevo León (Municipio Galeana, Cerro Potosí, shelter of thickets below timberline, 11,700 ft, *Schneider 1033* (F)). Specimen from Sweden (*F. Ahlberg s.n.*, ca. 1869 (US)) probably escaped from cultivation.

Maianthemum stellatum is the only species of the Linnaean genus *Convallaria* without a type at LINN. Specimens annotated "*C. stellata*" in other Linnaean depositories are of material evidently annotated after 1753. Linnaeus made no mention of *M. stellatum* prior to his description in *Species Plantarum*, although it had been cultivated in England and Europe since the early seventeenth century (Aiton, 1814), and he most likely had seen it at one time or another. In *Species Plantarum* Linnaeus cited published illustrations of *M. stellatum* found in Morison (1699) and Cornut (1635) and probably based his description on these. The illustrations in Morison are copies of the earlier illustrations in Cornut, so I have chosen Cornut's most representative illustration as the lectotype.

My treatment of *Maianthemum stellatum* is similar to that of Galway (1945) in that I find no basis to maintain any taxonomic rank for any of the variants found in the western United States. In California and Oregon *M. stellatum* exhibits considerable diversity of form, especially in leaf outline, and botanists in the region have occasionally recognized one or more varieties or species within this range. Greene, in particular, thought that there were two very definite species in the upper and lower Sierras, distinguished chiefly by subtle differences in leaf coloration, indumentum, and fruit color. Only fruit coloration could be of significance, but Greene based his observations on herbarium

specimens, which are quite unreliable with regard to color constancy. Plants from Oregon and California generally have longer pedicels than do individuals from more eastern states, but this feature is not correlated with any other, and the range of pedicel length is large even in the West. Considering the very broad distribution of this species, it is somewhat surprising that more variation is not exhibited. Three distinctive features (extended rhizome, dimorphic roots, and striping on immature berries) are evidently constant throughout the entire range. The singularity of these features and the constancy of their occurrence further support the recognition of a single broadly distributed species.

15. **Maianthemum trifolium** (L.) Sloboda, Rostlinnictví, 192. 1852 (*fide* Holub, 1974). FIGURE 20, MAP 10.

Convallaria trifolia L. Sp. Pl. 316. 1753; *Smilacina trifolia* (L.) Desf. Ann. Mus. Natl. Hist. Nat. **9**: 52. 1807; *Asteranthemum trifoliatum* (L.) Kunth, Enum. Pl. **5**: 153. 1850; *Tovaria trifolia* (L.) Necker ex Baker, J. Linn. Soc., Bot. **14**: 565. 1875; *Unifolium trifolium* (L.) E. Greene, Bull. Torrey Bot. Club **15**: 287. 1888; *Vagnera trifolia* (L.) Morong, Mem. Torrey Bot. Club **5**: 114. 1894; *Asteranthemum trifolium* (L.) Niewl. Amer. Midl. Naturalist **3**: 109. 1913. TYPE: [Soviet Union, Siberia?, 1740–1750?] (lectotype, here chosen, LINN 436.6).

Vagnera pumila Standley, Smithsonian Misc. Collect. **56**(33): 1. 1912. TYPE: Canada, Alberta, Prairie Creek, 3 July 1911, *Riley 100* (holotype, US (US no. 622636!); isotype, US (US no. 690417!)).

Vagnera trifolia (L.) Desf. f. *bifolia* Farw. Bull. Torrey Bot. Club **42**: 358. 1915. TYPE: United States, Michigan, Keweenaw Peninsula, 16 July 1886, *Farwell 3782*, *pro parte* (holotype, MICH).

Vagnera trifolia (L.) Desf. f. *unifolia* Farw. Bull. Torrey Bot. Club **42**: 358. 1915. TYPE: United States, Michigan, Keweenaw Peninsula, 16 July 1886, *Farwell 3782*, *pro parte* (holotype, MICH).

Aquatic herb, 4–15 cm tall. Roots uniform, 2 per node, 10–30 cm by 0.5–1 mm. Rhizome an irregularly branched sympodium, the individual units cylindrical, 2–30 cm by 1–2 mm, the scale leaves 3 to 10, the internodes 1–50 mm long, shorter apically, the lateral buds 1 at every node, axillary, 1 to 4 (to 8) forming renewal shoots; epidermis persistent; starch found only near rhizome apex. Leafy stem upright, 10–25 cm long, 2–3 mm broad at base, lower portion usually submersed, the surface smooth, glabrous; foliage leaves 2 to 4; internodes 3–6 cm long. Leaves clasping, sessile; blade elliptic, 5–12 by 2.5–4 cm (rarely 1 by 3 cm), the apex acute to acuminate, the base narrowly tapering to subpetiolate, the margin flat, with denticles distinct, the veins of uniform strength or weakly ranked, the surfaces glabrous. Inflorescence a simple raceme with 5 to 15 flowers; main axis upright, stiff, straight, 4–7 cm long, 1–2 mm wide at base, round or sometimes flattened, smooth, green, glabrous; internodes 5 to 15, 3–6 mm long, flowers arranged in helix. Flowers trimerous; pedicel spreading to arched-ascending, 1–3 by 0.5 mm, smooth, glabrous, with 1 bract subtending, additional 1 at right angles to first and either at pedicel base or midpoint; tepals uniform, spreading, 2.5–4 by 1.5–2 mm, white; stamens inserted at tepal base, the filament 1.5–2 mm long, thin, the anther 0.5–0.7 mm long; ovary spherical or cylindrical, 2–2.5 by 1.5–2.4 mm, the style 0.5–1.5 mm long, the stigma distinctively 3-lobed, 0.6 mm broad. Fruits spher-

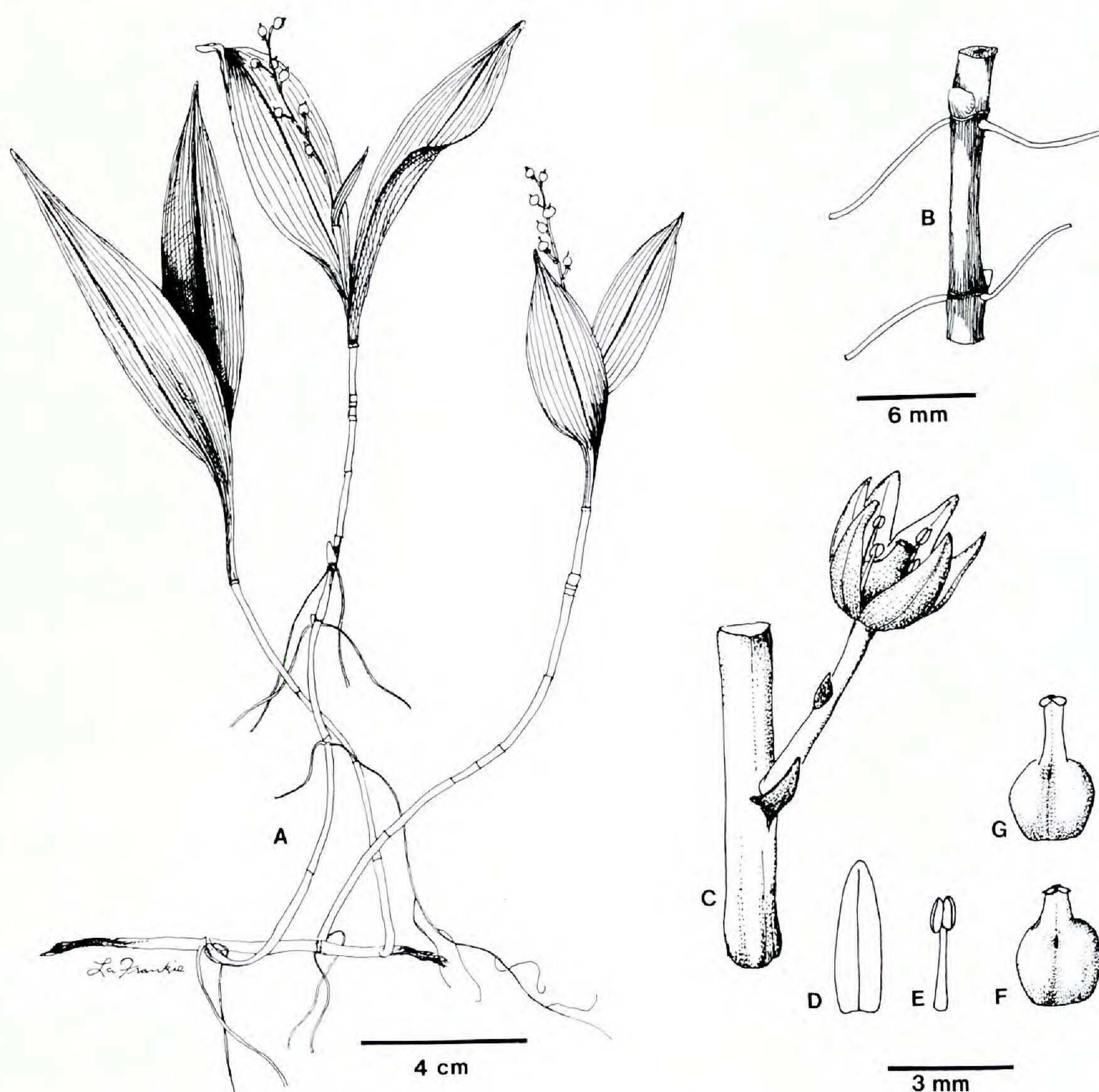
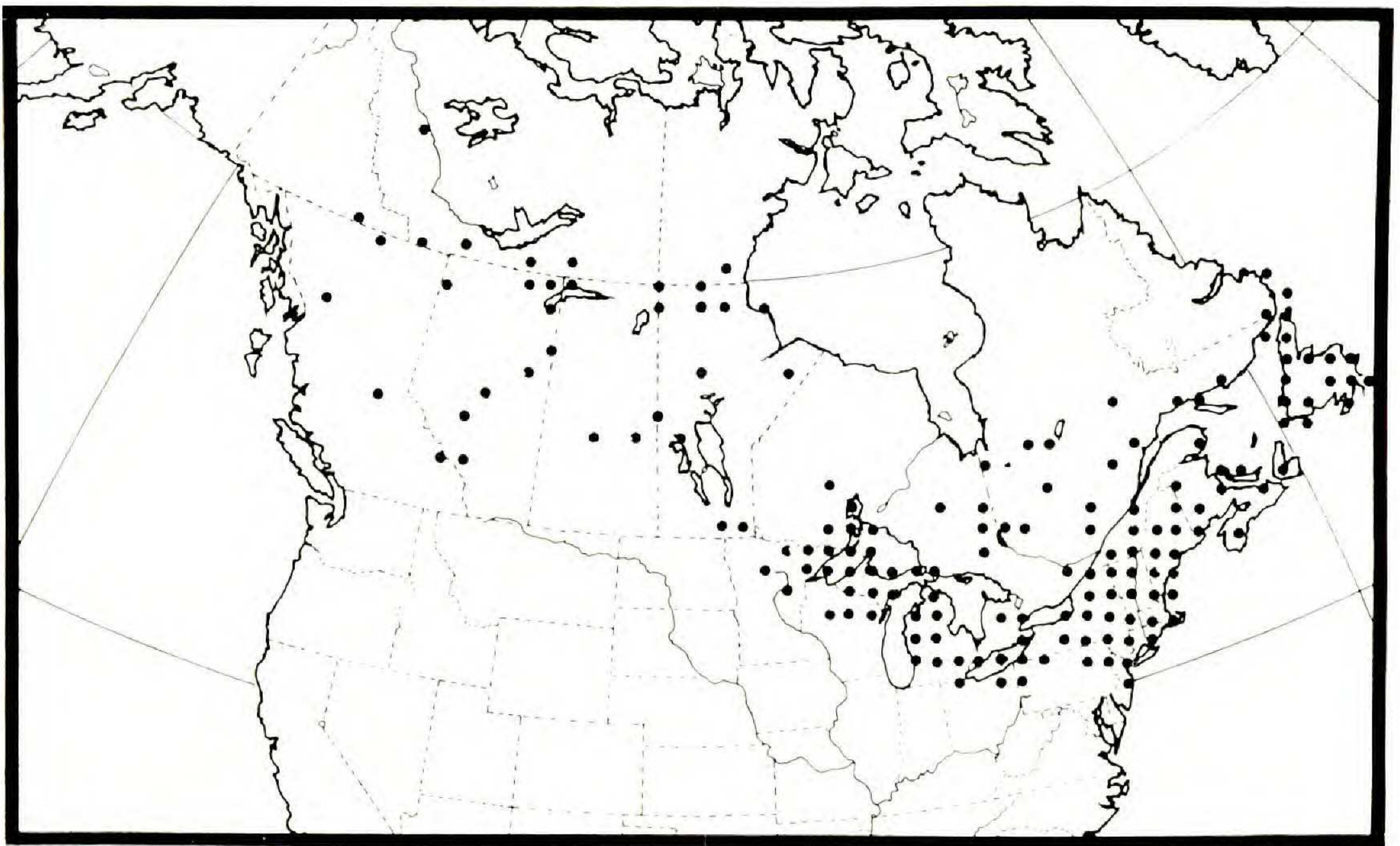


FIGURE 20. *Maianthemum trifolium* (LaFrankie 83-VI-12A, GH): A, rhizome, vegetative and fruiting shoots; B, detail of rhizome nodes; C, flower; D, tepal; E, stamen; F, G, gynoecia, showing variation in style length.

ical, 4–6 mm in diameter, green when young, maturing to red; seeds up to 3, spherical, 2 mm in diameter. Chromosome number $2n = 36$ (Kawano & Iltis, 1966).

ECOLOGY AND DISTRIBUTION. Clonal; sphagnum bogs, muskegs, and wet forests; sea level to 1000 m alt. Flowering May–June; fruits retained through August or September.

Eastern limit extending from Labrador (Salmon Bight, 53°27'N, 55°47'W, *Porsild* 24 (GH); Brig Bay, *Fernald* 26518 (GH, PH)) to New Jersey (Sussex Co., Pine Swamp, *Griscom* 12041 (GH); Morris Co., Budd's Lake, *Heritage* s.n. (PH)). Southern limit extending through Pennsylvania (Monroe Co., sphagnum bog, 1 mi N of Tobyhanna, *Buser* 11562 (GH); Bedford Co. (Wherry *et al.*, 1979)), northern Ohio (Lorain, Cuyahoga, and Fulton counties—Braun, 1967), and southern Michigan (Kalamazoo and Washtenaw counties—Voss, 1972).



MAP 10. Distribution of *Maianthemum trifolium*.

Very common but infrequently collected in wet forests and bogs of lower Ontario. Northern limit extending through northern Ontario (Obijawa Provincial Park, near Siouk, *Anderson s.n.* (wis)) to northern Manitoba (vic. Churchill, *Schofield 6571* (WTU)) and west through Mackenzie Basin (Lake Athabasca, Shelter Point, 58°50'N, 110°50'W, *Raup 433* (GH)); rare in northern Alberta (2 mi SW of Fort Smith, Northwest Territories, 60°00'N, 111°53'W, *Cody 4021* (GH, WTU)) and Yukon Territory (E end of Watson Lake, ca. 60°05'N, 128°43'W, *Raup 11058* (GH)). Western limit in British Columbia (Germansen Landing of Omineca R., *McCabe 7732* (WTU); mi 370, Alaska Highway, *Szczawinski s.n.* (WTU)). Evidently absent from northwestern continental U. S. and Alaska but reappearing in Siberia and northern China.

Although *Maianthemum trifolium* is chiefly distributed in North America, Linnaeus knew the species only from eastern Asia. There are two specimens at LINN. Number 436.6 is a plant with three leaves, annotated “*Convallaria trifolia* 7” by Linnaeus and bearing the note “*Phallangium forte 5 Amm. Siberia*” on the back. Number 436.7 is a smaller plant with two leaves and a young infructescence, annotated “*Convallaria trifolia*” and bearing the symbol that indicates its origin in Kamchatka. I have chosen number 436.6 as the lectotype because the protologue describes the species as having three leaves, not two, and the origin is described as “*Siberiae sylvis*,” not Kamchatka. This specimen undoubtedly came from one of Linnaeus’s sources in Russia between 1740 and 1755, but I can find no published account concerning its origin. Although the note on the back of the specimen mentions J. Amman (“*Amm.*”), we cannot assume it to be one of his collections because the idea of the plant growing in “*sylvis*” is directly from Gmelin (1747). Therefore, it is likely that Linnaeus wrote the diagnosis using both the published descriptions of Amman (1739) and Gmelin and specimen 436.6.

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LITERATURE CITED

- AITON, W. T. 1814. *Epitome Hortus Kewensis*. Longman, Hurst, Rees, Orme, and Brown, London.
- AMMAN, J. 1739. *Stirpium rariorum in imperio Rutheno sponte provenientium*. Acad. Scientiarum, St. Petersburg.
- BAKER, J. G. 1875. Revision of the genera and species of Asparagaceae. *J. Linn. Soc., Bot.* **14**: 508–632.
- BARKLEY, T. M., ed. 1977. *Atlas of the flora of the Great Plains*. Iowa State Univ. Press, Ames.
- BARTON, L. V. 1944. Some seeds showing special dormancy. *Contr. Boyce Thompson Inst. Pl. Res.* **13**: 259–271.
- & E. M. SCHROEDER. 1942. Dormancy in seeds of *Convallaria majalis* L. and *Smilacina racemosa* (L.) Desf. *Contr. Boyce Thompson Inst. Pl. Res.* **12**: 277–300.
- BELL, A. D., & P. B. TOMLINSON. 1980. Adaptive architecture in rhizomatous plants. *J. Linn. Soc., Bot.* **80**: 395–403.
- BRAUN, E. L. 1950. *Deciduous forests of eastern North America*. Blakiston Co., Philadelphia.
- . 1955. The phytogeography of unglaciated eastern United States and its interpretation. *Bot. Rev. (Lancaster)* **21**: 297–375.
- . 1967. *Vascular flora of Ohio*. Vol. 1. The Monocotyledoneae. Ohio State Univ. Press, Columbus.
- BUTTERS, F. K. 1927. Studies in the genus *Maianthemum*. *Minnesota Stud. Pl. Sci.* **4**: 429–444.
- CONOVER, M. 1982. The vegetative morphology and development of the reticulate-veined Liliiflorae and their parallel-veined allies. Unpublished Ph.D. dissertation, Univ. Massachusetts, Amherst.
- CORNUT, J. 1635. *Canadensium plantarum*. Simon le Moyne, Paris.
- CURTIS, J. T. 1959. *The vegetation of Wisconsin*. Univ. Wisconsin Press, Madison.

- DEAM, C. 1940. Flora of Indiana. Department of Conservation, Division of Forestry, Indianapolis.
- DEEVEY, E. S. 1949. Biogeography of the Pleistocene. *Bull. Geol. Soc. Amer.* **60**: 1315–1416.
- DESFONTAINES, R. L. 1807. *Maianthemum*. *Ann. Mus. Natl. Hist. Nat.* **9**: 54, 55.
- DUNCAN, T. 1983. Antonio Bertoloni's herbarium and the Florula Guatimalensis types. *Taxon* **32**: 299–301.
- EMONS, R. 1945. A revision of the Central American species of *Smilacina*. *Ann. Missouri Bot. Gard.* **32**: 395–408.
- ENGLER, A. 1888. Liliaceae. *In*: A. ENGLER & K. PRANTL, eds., *Nat. Pflanzenfam.* II. **5**: 8–92.
- FARWELL, O. A. 1915. Notes on Michigan Liliaceae. *Bull. Torrey Bot. Club* **42**: 351–358.
- FASSETT, N. C. 1935. A study of *Streptopus*. *Rhodora* **37**: 88–113.
- FERNALD, M. L. 1938. New and noteworthy plants of southeastern Virginia. *Rhodora* **40**: 404–407.
- GALWAY, D. 1945. The North American species of *Smilacina*. *Amer. Midl. Naturalist* **33**: 644–666.
- GMELIN, J. G. 1747. *Flora Sibirica*. Vol. 1. Acad. Scientiarum, St. Petersburg.
- GORHAM, A. L. 1953. The question of fertilization in *Smilacina racemosa* (L.) Desf. *Phytomorphology* **3**: 44–50.
- GRAHAM, A. 1973. History of the arborescent temperate element in the northern Latin American biota. Pp. 301–314 *in* A. GRAHAM, ed., *Vegetation and vegetational history of northern Latin America*. Elsevier, New York.
- GREENE, E. 1889. New or noteworthy species. IV. *Pittonia* **1**: 280, 281.
- HARA, H. 1975. The status of the genus *Oligobotrya* (Liliaceae). *J. Jap. Bot.* **50**: 225–227.
- HARVILL, A. M., C. E. STEVENS, & D. M. WARE. 1977. Atlas of the Virginia flora. Part 1. Virginia Botanical Associates, Farmville, Virginia.
- HEMSLEY, W. B. 1879–1888. *Biología Centrali-Americana, botany*. Vols. 1–5. R. H. Porter and Dulan and Co., London.
- HOLM, T. H. 1899. *Podophyllum peltatum*. A morphological study. *Bot. Gaz. (Crawfordsville)* **27**: 419–433.
- . 1929. The application of the term “rhizome.” *Rhodora* **30**: 6–17.
- HOLUB, J. 1974. Neglected plant names from the book “Rostlinictvi” by D. Sloboda. *Preslia* **46**: 167–171.
- INGRAM, J. 1966. Notes on the cultivated Liliaceae. 3. *Maianthemum*. *Baileya* **14**: 50–59.
- KANA, T. 1983. Studies in population demography of *Maianthemum canadense*. Unpublished Ph.D. dissertation, Harvard Univ., Cambridge, Massachusetts.
- KAWANO, S., M. IHARA, & M. SUZUKI. 1968a. Biosystematic studies on *Maianthemum* (Liliaceae-Polygonateae [*sic*]). II. Geography and ecological life history. *Jap. J. Bot.* **20**: 35–65.
- , ———, & ———. 1968b. Biosystematic studies on *Maianthemum* (Liliaceae-Polygonateae [*sic*]). IV. Variation in gross morphology of *M. kamtshaticum* [*sic*]. *Bot. Mag. (Tokyo)* **81**: 473–490.
- , ———, ———, & H. ILTIS. 1967. Biosystematic studies on *Maianthemum* (Liliaceae). I. Somatic chromosome number and morphology. *Bot. Mag. (Tokyo)* **80**: 345–352.
- & H. ILTIS. 1966. Cytotaxonomy of the genus *Smilacina*. II. Chromosome morphology and evolutionary consideration of the New World species. *Cytologia* **31**: 12–28.
- & M. SUZUKI. 1971. Biosystematic studies on *Maianthemum* (Liliaceae-Polygonateae [*sic*]). VI. Variation in gross morphology of *M. bifolium* and *M. canadense* with special reference to their taxonomic status. *Bot. Mag. (Tokyo)* **84**: 349–361.

- , ———, & S. KOYIMA. 1971. Biosystematic studies on *Maianthemum* (Liliaceae-Polygonateae [*sic*]). V. Variation in gross morphology, karyology and ecology of North American populations of *M. dilatatum* sensu lato. Bot. Mag. (Tokyo) **84**: 299–318.
- LAFRANKIE, J. V., JR. 1984. Anatomy of stem abscission in the genus *Smilacina* (Liliaceae). J. Arnold Arbor. **65**: 563–570.
- . 1985a. A note on seedling morphology and establishment growth in the genus *Smilacina* (Liliaceae). Bull. Torrey Bot. Club **112**: 313–317.
- . 1985b. Morphology, growth and vasculature of the sympodial rhizome in *Smilacina racemosa* (Liliaceae). Bot. Gaz. (Crawfordsville) **146**: 534–544.
- . 1986. Transfer of the species of *Smilacina* Desf. to *Maianthemum* Wigg. (Liliaceae). Taxon **35**: 584–589.
- LINNAEUS, C. 1737. Hortus cliffortianus. Amsterdam.
- . 1753. Species plantarum. Laurentii Salvii, Stockholm.
- MARTIN, P. S., & B. E. HARRELL. 1957. The Pleistocene history of the temperate biotas in Mexico and eastern United States. Ecology **38**: 468–480.
- MIRANDA, F., & A. J. SHARP. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology **31**: 313–333.
- MOHLENBROCK, R., & D. LADD. 1978. Distribution of Illinois vascular plants. Southern Illinois Univ. Press, Carbondale.
- MORISON, R. 1699. Plantarum historiae universalis. Theathro Sheldoniano, Oxford.
- OKUYAMA, S. 1935. On Japanese *Majanthemum*. J. Jap. Bot. **11**: 51–55.
- RADFORD, A. E., H. E. AHLES, & C. R. BELL. 1968. Manual of the vascular flora of the Carolinas. Univ. North Carolina Press, Chapel Hill, North Carolina.
- RICKETT, H. W. 1966. Wild flowers of the United States. Vol. 1. The northeastern states. New York Botanical Garden and McGraw-Hill Book Co., New York.
- . 1972. Wild flowers of the United States. Vol. 5. The northwestern states. New York Botanical Garden and McGraw-Hill Book Co., New York.
- SEN, S. 1974. Chromosomal evolution in Polygonatae. Bull. Bot. Soc. Bengal **28**: 103–111.
- STEYERMARK, J. A. 1950. Flora of Guatemala. Ecology **31**: 368–372.
- . 1963. Flora of Missouri. Iowa State Univ. Press, Ames.
- TAKAHASHI, M., & K. SOHMA. 1983. Pollen morphology of the genus *Smilacina* (Liliaceae). Sci. Rep. Tôhoku Imp. Univ., Ser. 4, Biol. **38**: 191–218.
- THERMAN, E. 1956. Cytotaxonomy of the tribe Polygonatae. Amer. J. Bot. **43**: 134–142.
- TOMLINSON, P. B., & E. S. AYENSU. 1968. Morphology and anatomy of *Croomia pauciflora* (Stemonaceae). J. Arnold Arbor. **49**: 260–275.
- UTECH, F., & S. KAWANO. 1976. Biosystematic studies on *Maianthemum* (Liliaceae). VIII. Floral anatomy of *M. dilatatum*, *M. bifolium*, *M. canadense*. Bot. Mag. (Tokyo) **89**: 145–157.
- VALENTINE, D. H., & H. M. HASSAN. 1971. Cytotaxonomy of the genus *Maianthemum*. J. Indian Bot. Soc. **50**: 437–446.
- VOSS, E. 1972. Michigan flora: part 1. Gymnosperms and monocotyledons. Cranbrook Institute of Science, Bloomfield Hills, Michigan.
- WHERRY, E., J. FOGG, & H. WAHL. 1979. Atlas of the flora of Pennsylvania. Morris Arboretum, Univ. Pennsylvania, Philadelphia.
- WOODSON, R. E., & R. W. SCHERY. 1940. Contributions toward a flora of Panama. IV. Miscellaneous collections, chiefly by Paul H. Allen. Ann. Missouri Bot. Gard. **27**: 265–364.
- & ———. 1945. Flora of Panama. Part 3 (Juncaceae–Marantaceae). *Ibid.* **32**: 1–105.